

CUPULADRIA CANARIENSIS (BUSK)—PORTRAIT OF A BRYOZOAN

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ABSTRACT. The lunulitiform bryozoan *Cupuladria canariensis* (Busk) is a benthonic marine organism, whose calcareous colonies can easily be recognized with a hand-lens or under the microscope.

This species is eurybenthic (2–> 300 fathoms), eurythermal (12–31° C.), reasonably euryhaline (28–37‰), and requires a stable quartz and/or carbonate sand bottom. It is at present widely distributed over the continental shelves of the Atlantic and East Pacific between the 14° C. surface isocrymes and had an equally wide distribution during the Late Tertiary and Quaternary.

The occurrence of *C. canariensis* in Miocene and Pliocene marine sediments of the southern part of the North Sea basin calls for sea-water surface temperatures at least 9° C. higher than those obtaining at present in this area. Its occurrence in the Miocene, Pliocene, and Early Pleistocene marine sediments of Spain, Italy, and Rhodes suggests that the Mediterranean was somewhat less saline in the geological past than it is at present.

Although lunulitiform Bryozoa range from the Upper Cretaceous to Recent, *C. canariensis* first appears in the Lower Miocene (Aquitanian). Its presence or absence among lunulitiform bryozoan assemblages may serve as a criterion for establishing the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic. On this criterion a large part of the 'Caribbean Oligocene' is to be considered as Lower Miocene.

Cupuladria canariensis was named in 1859 by the English bryozoologist George Busk, who discovered it in material collected from the sea bed in the neighbourhood of Madeira and the Canary Islands. Later in the same year he reported its occurrence in the Pliocene Coralline Crag in East Anglia. In the last hundred years the number of records has increased enormously, and the data are widely dispersed in the biological and palaeontological literature. It seemed worth while to try to assemble these widely scattered data so as to give a comprehensive picture of the species in space and time.

Such a synthesis is of considerable geological interest. It will be shown that a study of *Cupuladria canariensis* can not only give an insight into certain ecological, climatological, and hydrological conditions in the geological past, but can also help resolve the problem of determining the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf deposits.

Its interest for the palaeo-ecologist is implied in a variant of Grimsdale's golden rule for systematic palaeontologists: '... one detected synonym is worth from ten to one hundred new species' (1951, p. 467). Perhaps this account will help to establish that one ecologically well-known species is worth more than a hundred *tabulae rasae*.

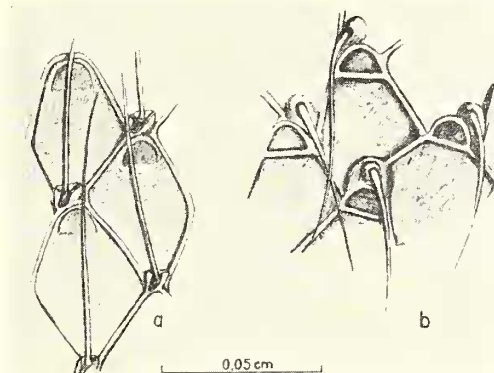
ZOOGEOGRAPHY AND ECOLOGY

1. Distribution

Cupuladria canariensis (Bryozoa: Cheilostomata, Anasca) belongs to the so-called lunulitiform Bryozoa (Pl. 25, fig. 1), all of which possess the same zoarial form as the genus *Lunulites* Lamarck, 1816. The fully grown colony, or zoarium, has the shape of a dome or flattened cone and consists of a single layer of cells, or zooecia, opening on the convex side of the dome. In addition to the normal cells, or autozooecia, in which

the polypides reside, there are other cells, the vibracula, each bearing a long, whip-like vibracular seta. In the genus *Cupuladria* there is, without exception, a vibraculum situated distally to each autozooecium; the tip of each seta is capable of describing a 180° arc in the median plane of its autozooecium (text-fig. 1).

Practically nothing is known with certainty concerning the function of these setae. It has been suggested, notably by Busk (1854, pp. 100, 104, 106; 1859, p. 79), that in certain lunulitiform species the setae might be 'subserving to locomotion'. Alternative



TEXT-FIG. 1. *a*, *Cupuladria canariensis*; *b*, *Discoporella umbellata*.
Vibracula with vibracular setae (after Norman 1909).

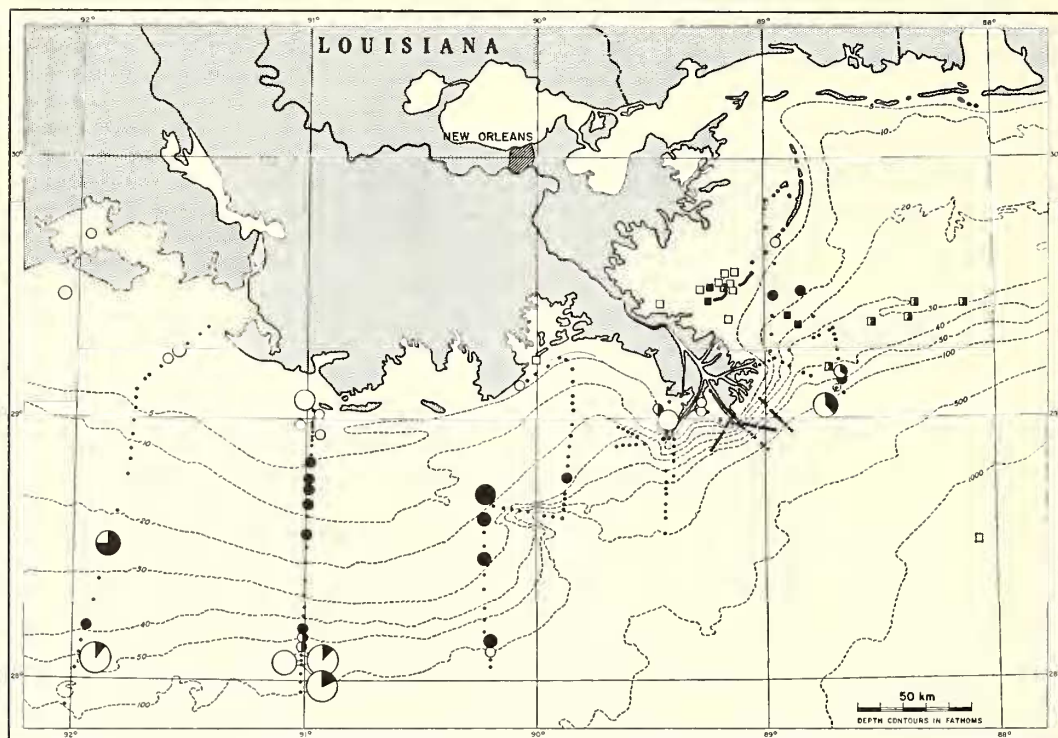
views are that they function as defensive or cleansing organs (Busk 1859, p. 79). In my opinion, it is clear that they serve to stir up the water in the colony's immediate vicinity, not so much in order to fan food particles towards the polypides' mouths as to prevent clay particles settling on the colony.

If this view is correct, then the possession of these setae must be a valuable asset to the lunulitiform Bryozoa, since it would make them some of the least sensitive to clay sedimentation. It is certainly no coincidence that of all the possible zoarial growth-forms it is precisely two lunulitiform genera, *Cupuladria* and *Discoporella*, that venture most closely, on both sides, to the mouths of the Mississippi distributaries (text-fig. 2). On this map the distribution pattern of the Bryozoa can clearly be divided into three zones:

a. An inner zone between the shore and the 5 fathom line, in which swell and breakers begin to disturb the sea bottom. Here, where the water is turbulent, no lunulitiform Bryozoa occur (for reasons given on p. 187) though other types do, such as those that attach themselves to plants or shells.

b. An outer zone between the 50 and 100 fathom lines, having a steep slope and an irregular topography and situated on the outer edge of the continental shelf. Deposition of clay along the outer margin of many continental shelves is notoriously slight to non-existent (Kuenen 1939; Shepard 1948, p. 160), and the Gulf of Mexico is no exception (Phleger 1959, p. 650; 1960, p. 288). The low rate of deposition and the local presence of hard substrata explain why Bryozoa with other growth-forms have been able to settle in this zone.

c. A middle zone, which coincides with the broad plateau lying between the 5 and 50 fathom lines. A large part of the clay brought down to the sea by the Mississippi is deposited on this plateau, and it is in this area that only lunulitiform species of Bryozoa, being equipped with vibracular setae, are able to survive.



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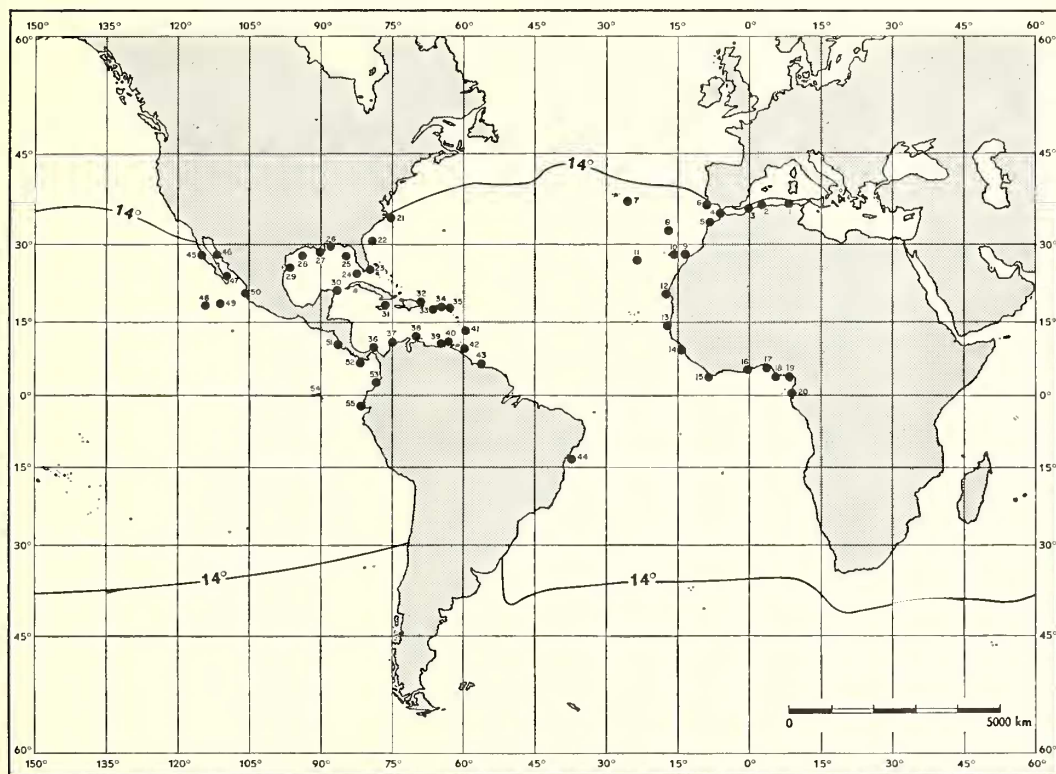
number of Bryozoa per 30 gramme sample	○ 1-3	barren sample	•
	○ 4-10	lunulitiform Bryozoa as percentage of total assemblage	●
	○ 11-30	lunulitiform Bryozoa present, but percentage unknown	◐
	○ 31-100		
	○ >100		
Bryozoa present, but in unknown quantity	◻		

TEXT-FIG. 2. Predominance of lunulitiform Bryozoa in the bottom sediments of the Mississippi Delta area. Sources: (a) collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk; (b) Parker 1956.

There are five characteristics which in combination are responsible for the ability of this type of bryozoan to occupy an exceptionally wide range of environments:

- (i) The ability to tolerate a certain amount of clay sedimentation owing to the possession of vibracular setae.
- (ii) The ability to exist on almost any kind of bottom as long as the latter consists of small particles.

- (iii) The ability to withstand a wide range of temperatures (eurythermal).
- (iv) The ability to withstand moderate salinity variations (euryhaline).
- (v) An insensitivity to hydrostatic pressure, light penetration, and other factors directly concerned with depth.



TEXT-FIG. 3. Recent distribution of *Cupuladria canariensis*, showing confinement between 14° C. surface isocrymes (isocrymes after Sverdrup, Johnson and Fleming 1960 and Wust 1960).

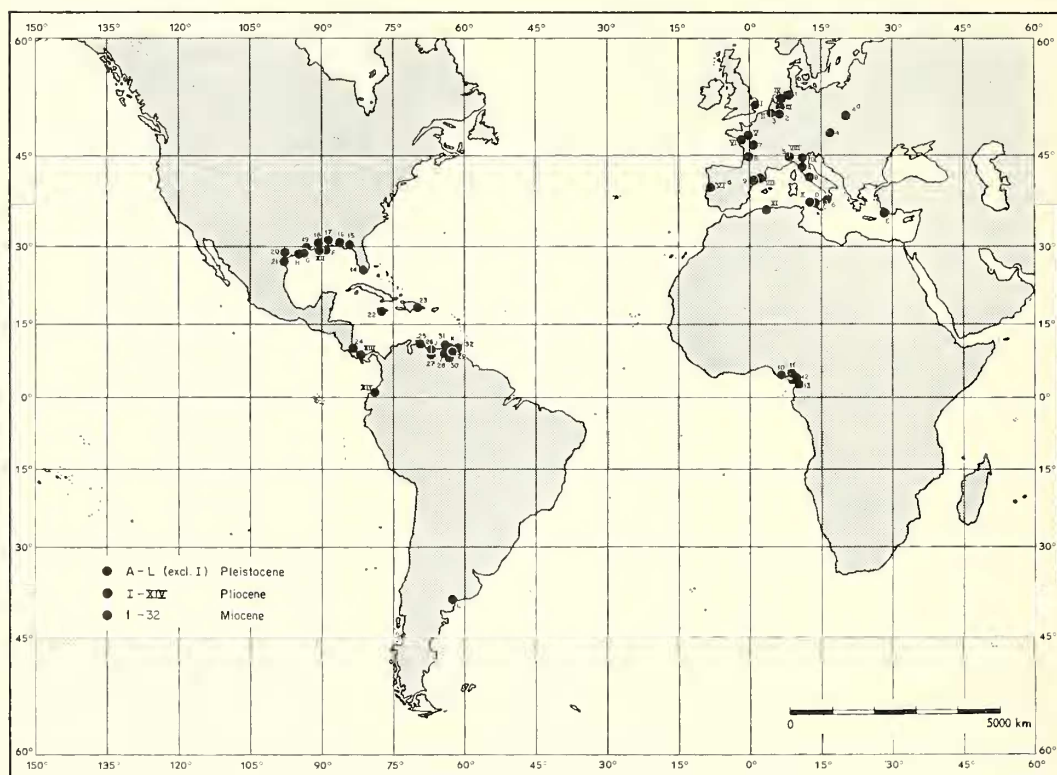
This combination of characteristics is the reason for the wide area of distribution of *Cupuladria canariensis*, which includes the tropical and subtropical Atlantic, the eastern Pacific, and the Mediterranean (text-fig. 3), and which has been generally the same throughout the Later Tertiary and Quaternary (text-fig. 4). Yet its distribution is not merely wide on a global scale. Within fairly restricted areas such as the Gulf of Mexico (text-figs. 5, 6) and the Nigerian shelf (text-fig. 7), or in the marine Pliocene of the Low Countries (text-fig. 8) and in the Miocene basin of eastern Venezuela (text-fig. 9), it is also widely distributed on a provincial scale.

2. Larval stage

One may wonder whether there is not perhaps a sixth characteristic contributing to this organism's wide distribution: the duration of its larval stage. Like all Bryozoa, the lunulitiforms are sessile, colonial organisms but they possess a free-swimming larval

stage. The larvae are able to swim by means of their cilia, and the duration of this free-swimming stage is conceivably one of the factors contributing to the geographical distribution of a benthonic species (Cloud 1959, p. 951).

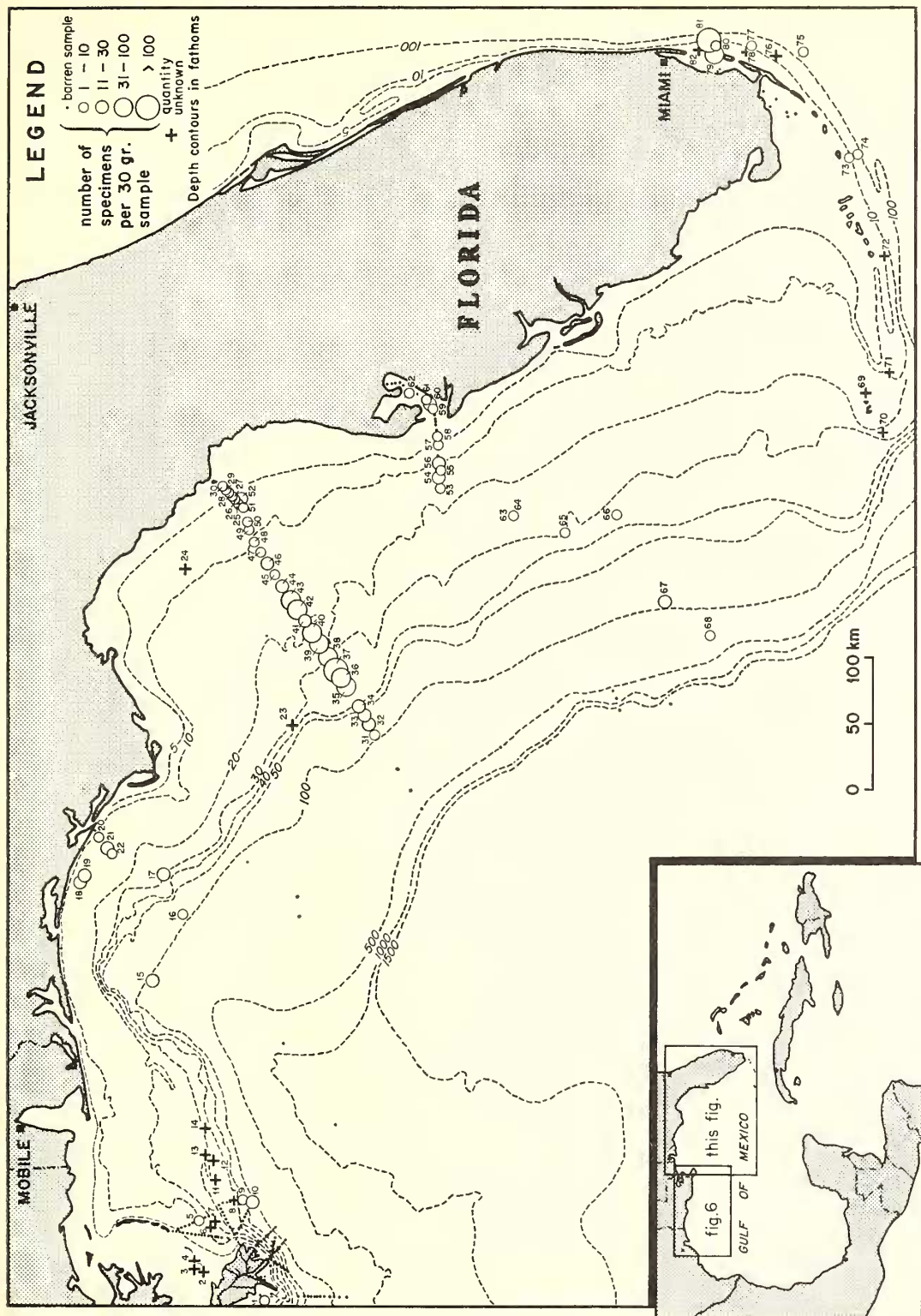
Unfortunately, the larval stage of *C. canariensis* is still unknown. Within the order Cheilostomata, however, two completely different types of larvae occur. One of these, the so-called *Cyphonautes* larva, which is characterized by the possession of a functional



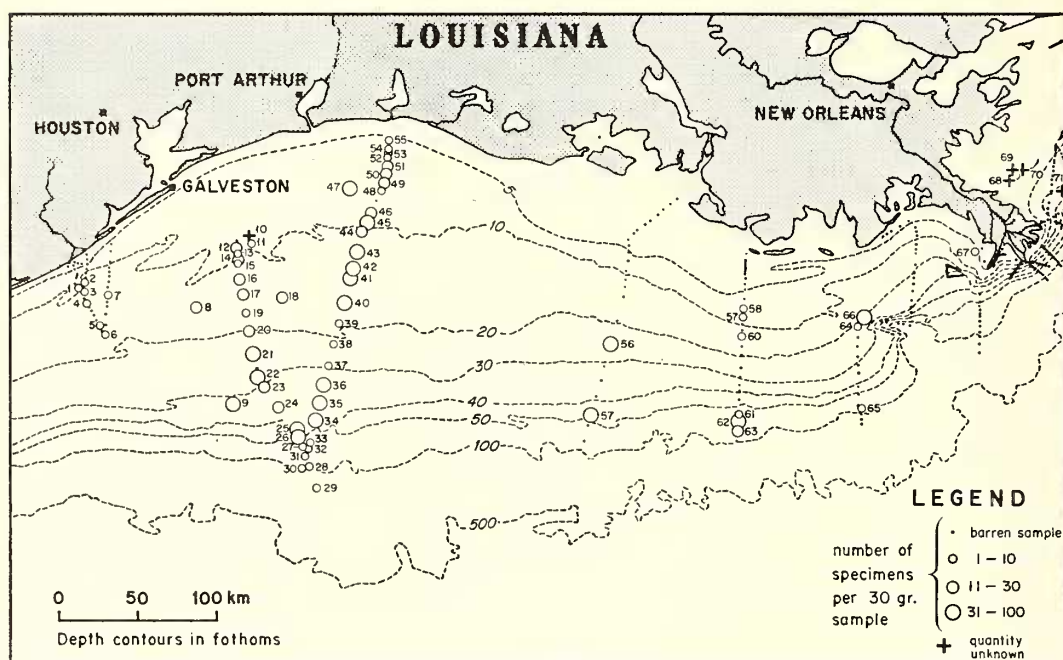
TEXT-FIG. 4. Fossil distribution of *Cupuladria canariensis*.

alimentary canal, may spend a period of up to two months in this condition. The large majority of the Cheilostomata, however, have the second type of larva, in which this structure is rudimentary or entirely lacking. According to current views, such larvae are therefore drastically limited in the duration of the free-swimming stage (to no more than 12–24 hours, depending on the supply of yolk), so that they do not become truly pelagic. Nevertheless, there are species of Cheilostomata that have this second type of larva and which, in spite of this, have a very wide, or almost cosmopolitan distribution (e.g. *Microporella ciliata*).

This is a baffling paradox with which every student of Bryozoa is sooner or later confronted and for which various solutions have been proposed, e.g. continental drift, dispersal via ancient archipelagos or shelf bridges, or trans-oceanic rafting on floating objects by surface currents. Recently Cheetham (1960), in a stimulating paper, discussed

TEXT-FIG. 5. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the north-eastern Gulf of Mexico.

the merits of each of these three hypotheses in the light of Early Tertiary cheilostome distribution. He clearly favours the third alternative, but did not fully consider the possibility of long-distance dispersal in the larval stage. Yet it is precisely this fourth alternative that most strongly suggests itself in the case of those zoarial form-groups that are most unlikely to become attached to seaweed or other 'rafts'. If the distribution of such species, including *C. canariensis*, is amphi-Atlantic, and if the Wegenerian hypothesis that the surface and bottom configuration of the Miocene Atlantic Ocean were drastically



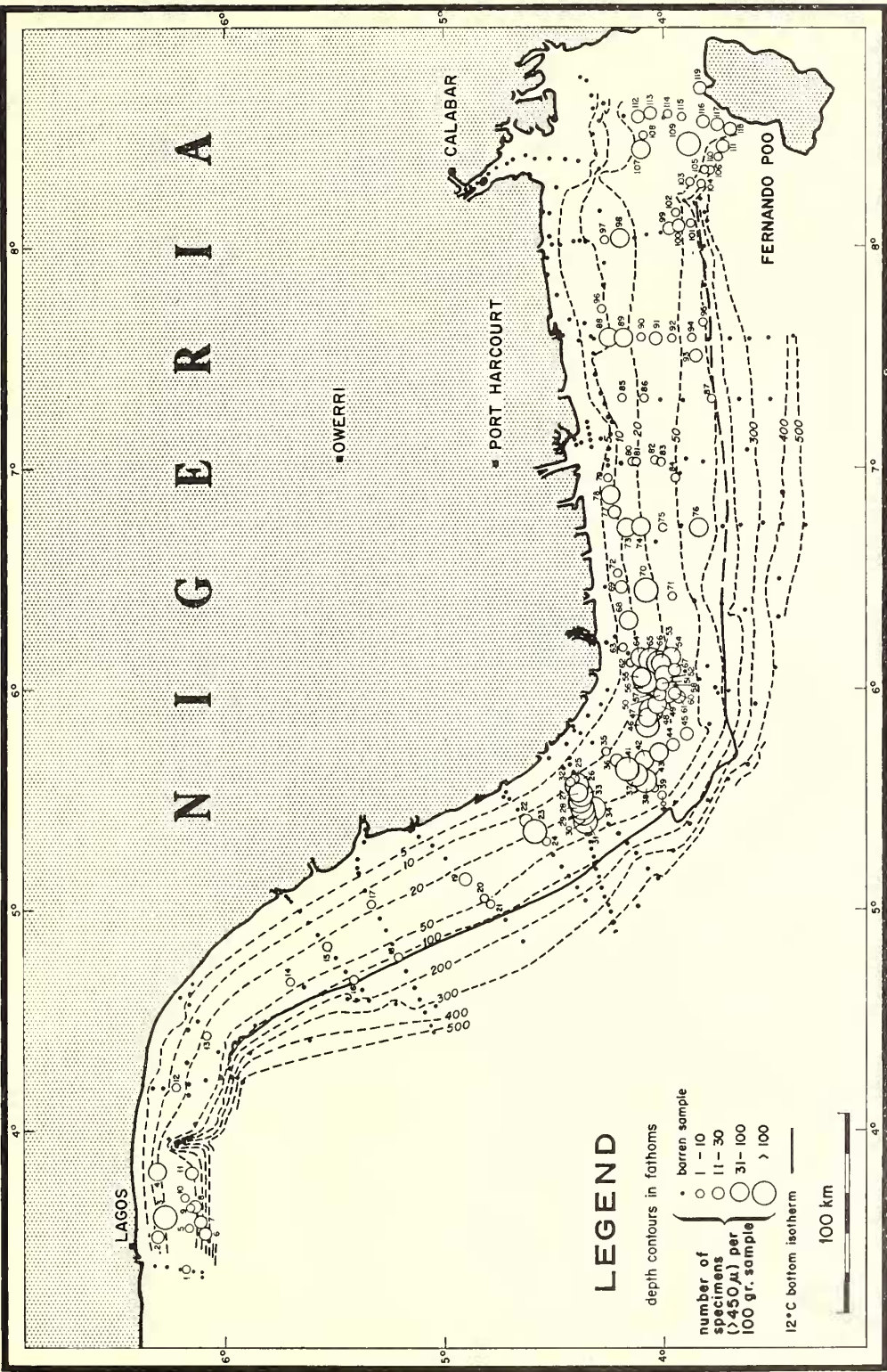
TEXT-FIG. 6. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the north-western Gulf of Mexico.

different is rejected, the conclusion is inevitable that their free larval stage must under certain conditions be, and have been, able to last a long time.

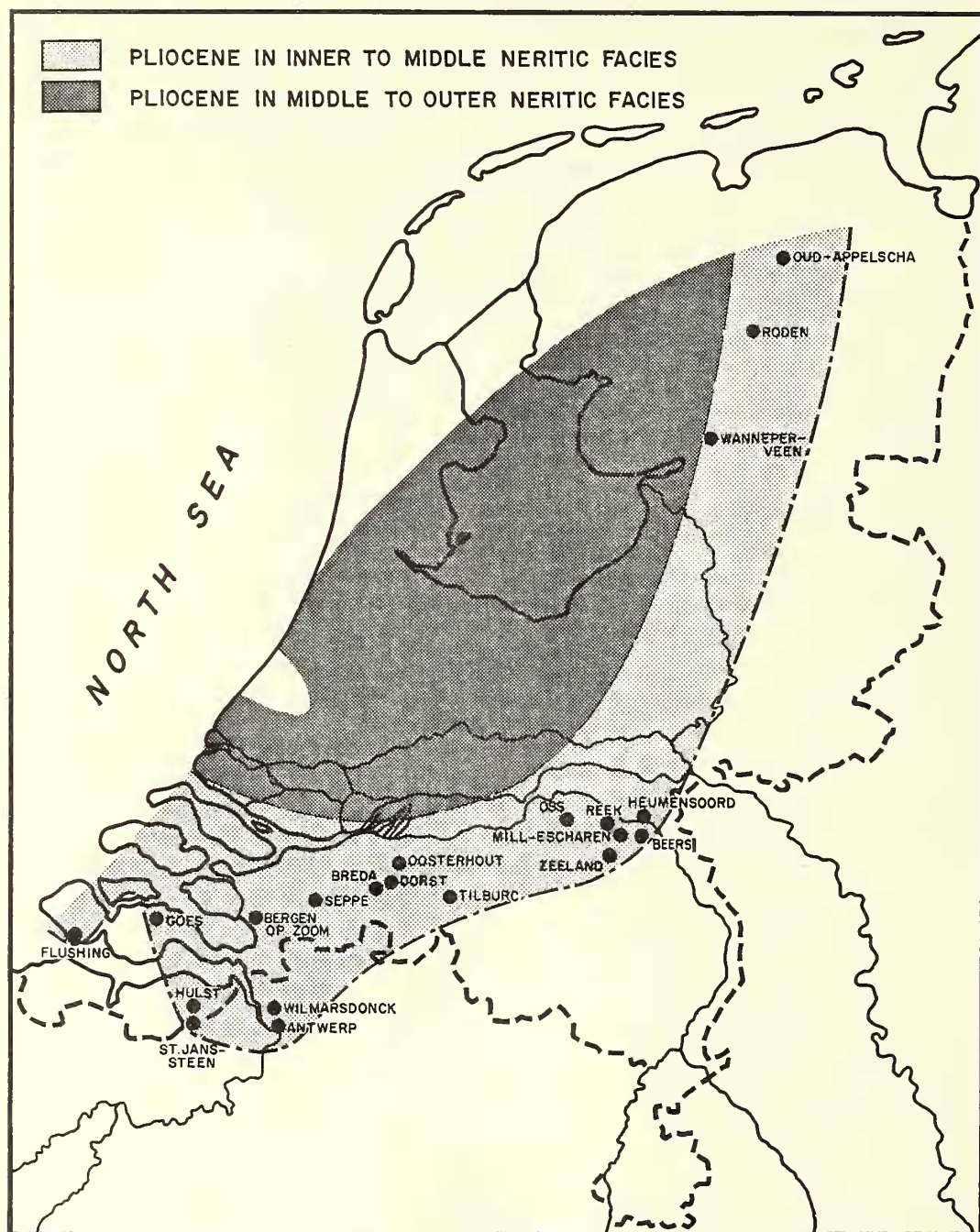
Harmer (1910, p. 520) suggested 'that it does not follow that because we know that a larva may, under favourable conditions, fix itself a few minutes after it becomes free, we should be justified in assuming that that larva would not retain for a long period the power of undergoing a normal metamorphosis should it be drifted away from suitable fixing-grounds'. Silén's (1944, pp. 30, 31) hypothetical concept of external food absorption in larvae which are devoid of an alimentary canal is also interesting in this connexion.

3. Substratum

After a brief or protracted period of wandering, the larva settles on a hard substratum. It would seem to make a very careful choice in this matter, as if it knew in advance that the substratum on which it settled would have to be raised above the sea floor and eventually become lodged in the apex of the conical structure which is the adult zoarium.

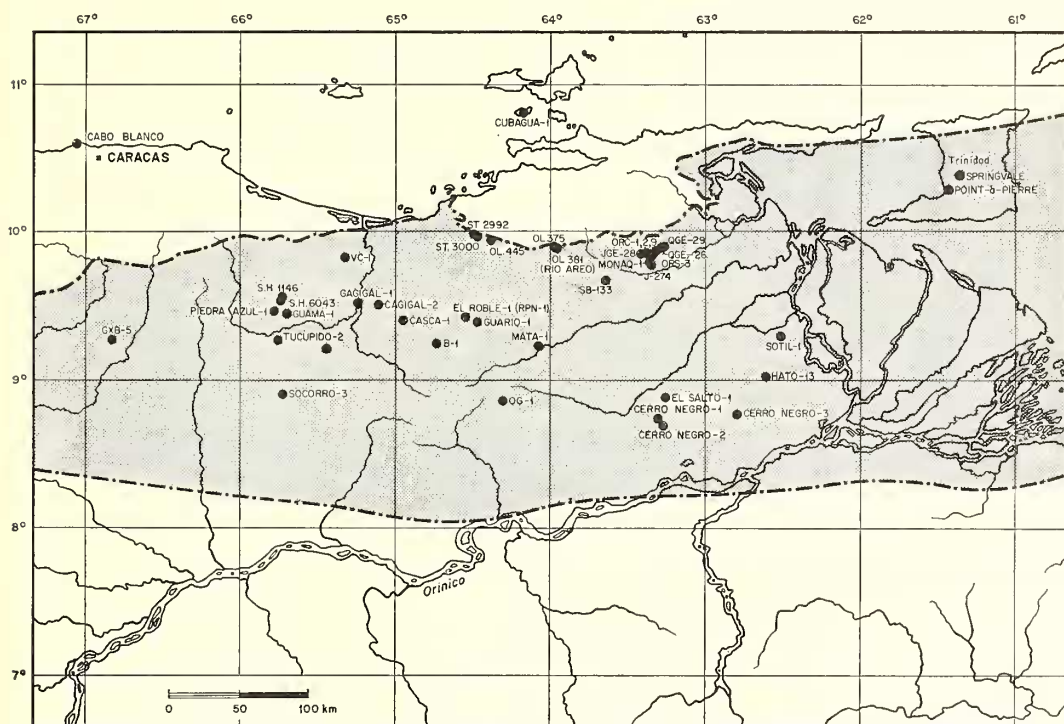


TEXT-FIG. 7. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the Nigeria shelf (12°C. bottom isotherm from data filed at KSEPL, Rijswijk).



TEXT-FIG. 8. Distribution of *Cupuladria canariensis* in the eastern part of the Pliocene North Sea basin (distribution of marine facies after van Voorthuysen 1956).

Above all, therefore, this substratum must not be too big, and it is for this reason that we usually find coarse quartz grains, glauconite pellets, small shell fragments, broken echinoid spines, even moderately large Foraminiferida such as *Amphistegina gibbosa* and *Globorotalia menardii*, or fragments of other lunulitiform Bryozoa functioning as nuclei for *Cupuladria*. The ideal biotope for the lunulitiform Bryozoa is therefore a small-particle (quartz and/or carbonate sand) bottom. They never occur on a bottom consisting



TEXT-FIG. 9. Distribution of *Cupuladria canariensis* in the Miocene basin of eastern Venezuela (shaded area).

entirely of clay, and are never found encrusting rocks, large pebbles, piles, larger shells, or other such large objects. It is not without reason that lunulitiform colonies are commonly called 'free' (though this is incorrect) as opposed to 'encrusting' forms. So unusual, in fact, is the appearance of an 'encrusting' *C. canariensis* that Silén (1942, p. 14) refers to a juvenile colony on a small stone from Anguilla in the West Indies as only 'possibly belong[ing] to this species'.

The question arises whether the larva's power of discrimination is real or apparent. On the one hand one might suppose that the larva settles indiscriminately on all kinds of substrata and that it develops into a colony only on those that are suitable. In that case the selection is the work of external circumstances and not of inherent 'intelligence' in the larvae. On the other hand, selectivity on the part of pelagic larvae has definitely been observed in other groups of marine invertebrates. According to Thorson (1955, p. 390), Wilson (1952 and earlier papers) has shown 'that the larvae of several polychaetes,

when ready to metamorphose, will critically examine the bottom substratum to which they are exposed. If they find it attractive, they settle. If they find it less attractive or directly repellent, they will continue their pelagic life for days or even weeks. During such a prolonged larval life these larvae test the substratum at intervals as they are transported by the current directly over the bottom.'

As far as *Cupuladria* is concerned, the following example is pertinent. Plate 25, figs. 2a, b, show two specimens of *Cupuladria* (not *C. canariensis*, but an allied species, having affinity with *C. pyriformis* Busk) from the subsurface Oficina formation (Miocene) of eastern Venezuela. The larvae of both specimens, and of several others from the same shale samples, originally singled out, and settled upon, specimens of *Planorbulinella trinitatensis* (Nuttall) and persistently neglected several other species of smaller Foraminiferida. This choice seems to have been prompted by the absence of quartz sand; for in a sandy facies with both quartz grains and *Planorbulinella* available in good quantities, such as is found along the southern boundary of the eastern Venezuela basin, settling invariably occurred on the quartz grains only.

4. *Astogeny*

Having attached itself to a suitable substratum, the larva then rapidly undergoes its metamorphosis into the first individual, the 'ancestrula', of the future colony. Further development takes place by a process of budding. It is interesting to follow the juvenile colony through the early stages of this development, especially since Harmer in 1931 (p. 162) was still able to say: 'there is no conclusive evidence with regard to the earliest stages in the discoidal or conical colonies, and a mere count of the number of surrounding zooecia is not enough to settle the matter', and no pertinent observations have been made since then.

By the time the number of zooecia has increased to twenty-six, the zoarium has passed through several separate stages of growth (text-fig. 10):

(a) *The single ancestrula*. Despite prolonged searching I have never observed a single ancestrula. Thus it would seem that the process of budding sets in very soon after the metamorphosis is complete.

(b) *The three-cell zoarium*. This, the earliest zoarial growth stage observed, invariably consists of three zooecia forming the pattern shown in text-fig. 10b. I have recorded several dozens of these three-cell colonies. They display distinct bilateral symmetry. From their mutual relationships it may be inferred that the ancestrula has given rise to two proximo-lateral first-generation zooecia.

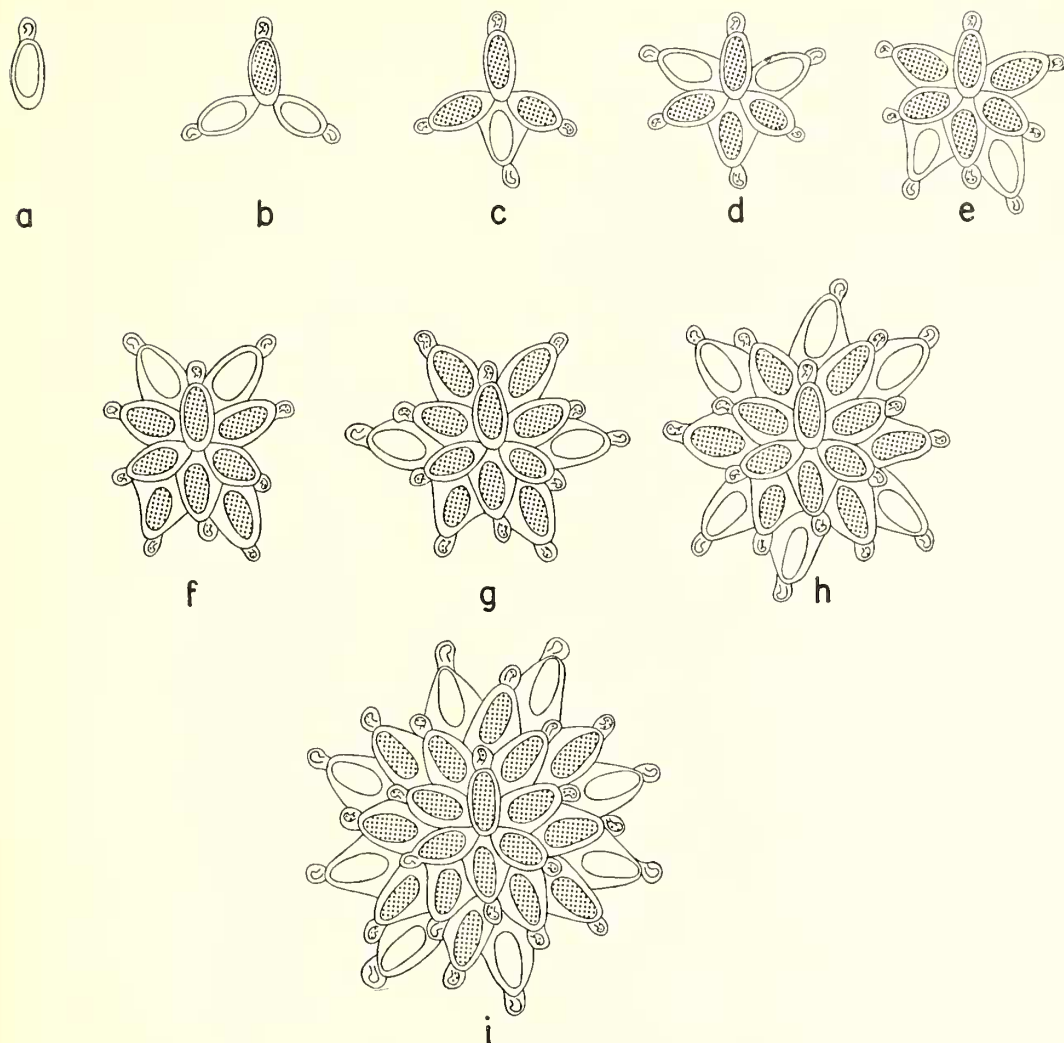
(c) *The four-cell zoarium*. A fourth zooecium is added proximally in the plane of symmetry (text-fig. 10c). The circle is closed and the colony is ready to start its radial growth.

(d) *The six-cell zoarium*. By the addition of two zooecia in the angles between the ancestrula and the two first-generation zooecia, the colony assumes the shape of a six-pointed star (text-fig. 10d). The plane of symmetry through the ancestrula is still clearly apparent.

(e) *The eight-cell zoarium*. Two new proximo-lateral zooecia appear (text-fig. 10e).

(f) *The ten-cell zoarium*. Two more zooecia are added distally, one on either side of the ancestrula (text-fig. 10f; Pl. 25, fig. 3).

(g) *The twelve-cell zoarium*. Two new lateral zooecia appear (text-fig. 10g). At this stage the colony is still markedly stelliform; the bilateral symmetry can be seen without



TEXT-FIG. 10. Early stages of zoarial growth in *Cupuladria canariensis* (based on a series of Recent specimens from Nigeria).

difficulty. No zooecia are yet in proximal contact with the vibracula of preceding cells, but this situation changes in the next stage. This earliest, central, part of the colony is therefore relatively less densely covered by vibracular setae than later, peripheral, additions. It is therefore probably no coincidence that preferably (although not exclusively) these central zooecia sometimes regenerate into large vibracula of the type first described by Hastings (1930, p. 714; see also Silén 1942, text-fig. 8), whereas in other lunulitiform species they tend to develop a calcareous closure.

(h) *The eighteen-cell zoarium.* Six new zooecia have appeared at the periphery (text-fig. 10h), probably via two intermediate stages. The first slight departure from the original plan of symmetry is now apparent, since the proximal and the distal indentations

at the periphery in the median line are too large to be filled by a single zooecium and yet too small to accommodate a pair of zooecia. The filling of the gap therefore takes place asymmetrically.

(i) *The twenty-six-cell zoarium.* A further departure from bilateral symmetry takes place (text-fig. 10i). By now the colony has attained a diameter of 1.9 mm. and is well on its way to adulthood.

Two points emerge from these observations:

- i. Waters's (1926, p. 426 and text-fig.) concept of a double ancestrula in *Cupuladria*, the two being turned in opposite directions, and each giving off three distal zooecia, is untenable. Although Waters specifically mentioned *C. canariensis* in connexion with his observations, it is clear from the occurrence of partially closed zooecia and from the provenance of his material (Princess Charlotte Bay, Queensland, Australia), that he was actually dealing with *C. guineensis* (Busk).
- ii. Silén's (1942) theory of spiral growth is no longer valid in the case of the genus *Cupuladria*.

I should like to emphasize that the astogeny outlined above only applies to ideal cases, and that deviations from this scheme are common and may appear at an early stage (Pl. 25, fig. 4). Usually such deviations are closely bound up with irregular configurations of the small-particle substratum, or with an excentric position of the ancestrula on the substratum. The eight-cell zoarium figured in Plate 25, fig. 4 deviates in that it has developed a zooecium (on the left) in a position that would normally not be occupied until the twelve-cell stage, while the usual place for the eighth zooecium (on the right-hand side) remains vacant. Occupation of the latter position, which projects beyond the edge of the particle, would have involved building a stronger dorsal wall than the extremely thin one required in the position now preferred, where it is supported by the substratum. Obviously less building energy is required for growth on the substratum than for expansion beyond its edges.

5. Mode of life of lumulitiform colonies

The mode of life of the adult colony and, closely connected with that, its orientation with respect to the sea bottom, are controversial matters, and widely differing suggestions

EXPLANATION OF PLATE 25

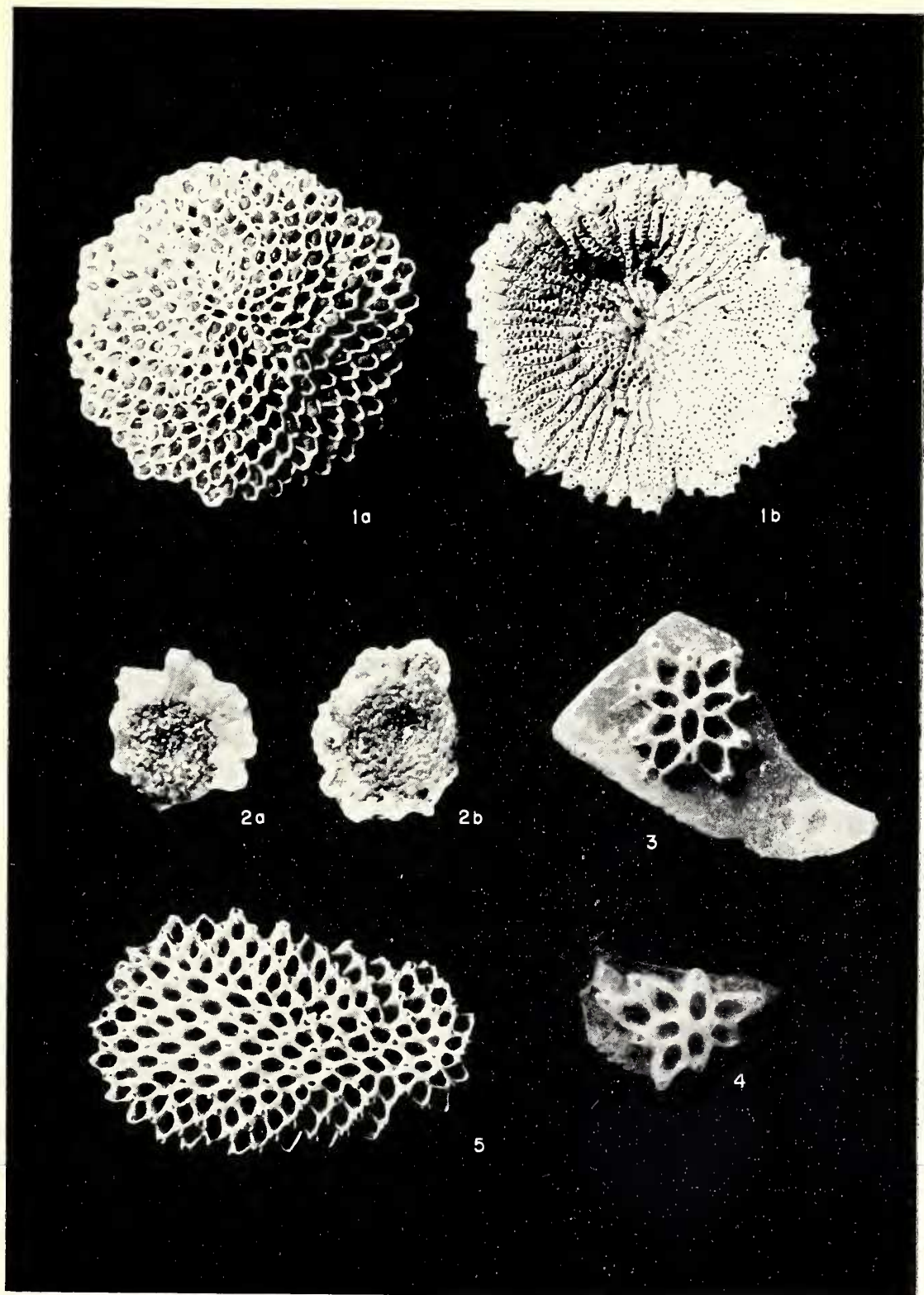
Fig. 1. *Cupuladria canariensis* (Busk). Adult colony. *a*, View of the convex surface; *b*, View of the concave surface. G.S. 173, Pliocene of Proefboring 41, Reek, Netherlands, 15.00–20.00 m. $\times 10$. (After Lagaaij 1952.)

Fig. 2. *Cupuladria* sp. Concave side of juvenile colonies, showing larval predilection for the foraminiferid *Planorbulinella trinitatis* (Nuttall). Lower Miocene (Oficina formation) of Texas Petroleum Company well Mata-1, Estado Anzoategui, Venezuela; *a*, 8,160–8,170 ft.; *b*, 8,300–8,320 ft. $\times 20$.

Fig. 3. *Cupuladria canariensis* (Busk). Juvenile colony (ten-cell stage) in normal symmetrical development. Recent, Mees Cremer 1959 Sta. 98, Nigeria, 14 fms. $\times 20$.

Fig. 4. *Cupuladria canariensis* (Busk). Juvenile colony (eight-cell stage), showing early departure from bilateral symmetry. Recent, Mees Cremer 1959 Sta. 376, Nigeria, 11 fms. $\times 20$.

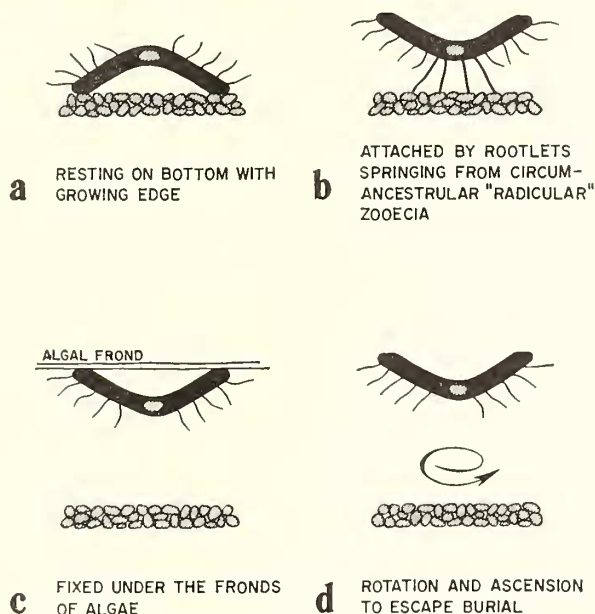
Fig. 5. *Cupuladria canariensis* (Busk). Regenerated colony, showing sector of original large flattened conical colony with peripheral outgrowth in radial direction. Recent, Râs-el-Amouch, Mediterranean, 45 fms. $\times 10$. (After Darteville 1935.)



LAGAATJ, *Cupuladria canariensis* (Busk)

have been made, none of which, according to Harmer (1931), have been supported by pertinent observations. Four tenable hypotheses have been put forward (text-fig. 11).

As Harmer (1931, pp. 150–1) has shown, the conventional view that the colony rests on its flat 'base' (text-fig. 11a) was first disputed by Maplestone (1910, p. 3), who expressed the opinion that 'the conical forms in their living state have the base uppermost'. Although at this time Maplestone was only referring to the conical colonies of the genus



TEXT-FIG. 11. Various hypotheses regarding the mode of life of lunulitiform colonies.

Conescharellina, later authors have extended his contention to include other genera whose colonies are conical. Moreover, Maplestone was not certain whether the conical colonies (of *Conescharellina*) hang point downwards from some foreign object, or whether they retain this position on the bottom by means of anchoring filaments.

Canu (1915, p. 21) adopted and elaborated on both hypotheses. His early reasoning is not generally known (cf. Harmer 1931, p. 151), but later re-statements of his views have profoundly influenced later workers. It is therefore necessary to quote Canu in full on this point: 'Les espèces flottantes comme les *Lunulites* ont le zoarium conique, la pointe en bas. Tantôt il est maintenu sous les Algues [text-fig. 11c], tantôt il est attaché à de petits objets par des radicelles [text-fig. 11b]. Celles-ci proviennent de *Zoécies radiculaires* (= *Zoécies* avortées de d'Orbigny) disposées autour de l'ancestrule. . . . Les zoécies radiculaires sont d'abord des zoécies hydrostatiques. La larve, en effet, se fixe sur un grain de sable; l'ancestrule qui se développe émet immédiatement des zoécies radiculaires qui l'enveloppent et permettent à l'animal de commencer son ascension sous une Algue loin du sable dangereux à son développement. . . . Soit attachés par des radicelles, soit retenus sous les Algues, les *Lunulites*, par leur forme turbinée, sont de position très instable: ils chavirent au moindre filet d'eau. L'animal maintient sa position

normale à l'aide de longs filaments articulés appelés *vibraculaires*. Ce sont donc des appareils de *stabilisation* un peu analogues au balancier des danseurs de corde.'

The same views, essentially unchanged, are repeated by Faura and Canu (1916), Canu and Bassler (1920, pp. 238 ff.), and Canu and Lecoindre (1927, p. 35). Waters (1921) was quick to oppose these views, which have in fact largely been confined to the French school. I refer in particular to his statement (1921, p. 401): '... though sometimes the growth is on a much larger stone, as in some specimens of *Cupuladria canariensis* from Petit Tahou, Liberia. It would seem impossible for a colony so heavily weighted to float, nor can we think it could float in a reversed position.' In 1926, however, Waters (1926, p. 425) wrote more cautiously: 'What we have called the upper surface is, in the ancestrular and early stages, at the top, even though there may be a subsequent reversal....'

Finally, Canu and Bassler, realizing how difficult it was to see how a conical colony with its apex downward could 'maintain its equilibrium even in the water, in a position absolutely contrary to the ordinary laws of statics', invoked rotation as a means of conserving its position (text-fig. 11d), first for *Conescharellina* (1929, p. 482) and later for *Lunulites* (1931, p. 9): 'Ils vivent donc l'apex en bas au voisinage du fond sableux. Ils s'en dégagent par rotation et ascension pour éviter l'enlissement', and (1931, p. 19) 'Les *Lunulites* sont de petites coupes en perpétuelle rotation pour se dégager du sable et changer de place'.

Darteville also attributed a planktonic mode of life to *Lunulites* (1933, p. 69) and to *Cupuladria* (1943, p. 108): 'Leur mode de vie est semblable à celui, bien connu, des *Lunulites*, c'est-à-dire que la colonie flotte entre deux eaux, les zoécies tournées vers le dessous, la face concave vers le haut. . . .' The designation 'face supérieure' for the concave side and 'face inférieure' for the convex, celluliferous side of lunulitiform colonies still persists in recent French literature (Vigneaux 1949; Buge 1957).

Darteville (1933, p. 57), moreover, provided a novel explanation of the role played by the small foreign particle at the downward directed apex of the cone: 'La présence de ce substratum constitué par un morceau de coquille, une nummulite, un grain de sable, contribue à maintenir l'équilibre de la colonie et à l'empêcher d'être chavirée par les vagues'; it served, in other words, as ballast, and as such would profoundly influence the shape of the colony. According to Darteville (loc. cit., p. 70) the lighter the substratum, the flatter the zoarial cone, and, conversely, the heavier the particle, the higher and more dome-shaped the colony would have to become in order to keep the ballast as low as possible: '... ce qui gouverne donc la colonie, c'est la souci d'éviter le renversement et de maintenir le meilleur équilibre possible au sein du fluide.'

Harmer's presidential address to the Linnean Society of London in 1931 made it abundantly clear that Canu and Bassler's reasoning was based entirely on inference and not on direct observation. He added (1931, p. 151): 'I have failed to find any evidence that is really conclusive with regard to the question at issue. Except for Whitelegge's very brief account, I am acquainted with no observations made on living specimens, and in my judgment the matter should for the present be regarded as undecided.' Harmer's statement is still as valid today as it was thirty years ago. Here is clearly a case where laboratory experiment could be of value. It should not be too difficult to collect some living specimens of *Cupuladria* and keep them under observation in a sea-water aquarium.

Another example of reasoning by inference, the emphasis in which is laid on the

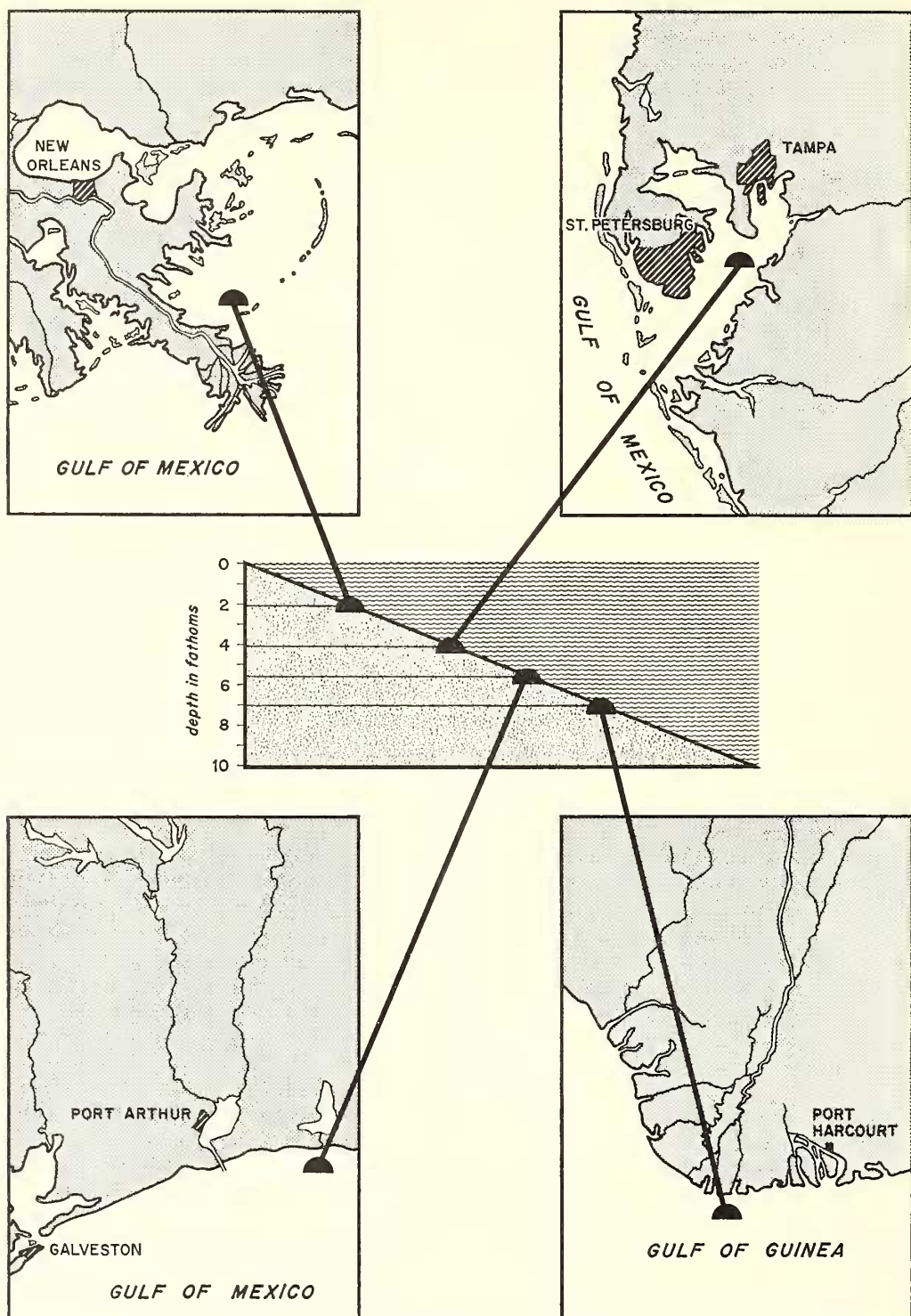
orientation of the ancestrula and of later zooecia with respect to the small-particle substratum, occurs in Silén (1947, pp. 5–6, 8, 15 and text-fig. 8). He concluded (correctly, in my opinion) that the colonies of *Cupuladria* rest freely on the sea bottom with the apex pointing upwards. Silén thereby reverted to the conventional view (see, however, Silén 1942, p. 13).

Two further arguments, both arising from the ecology of *C. canariensis*, support this conventional view, or rather conflict with the hypothesis of a planktonic mode of life postulated by Canu and his school. In the first place, if *C. canariensis* were indeed a planktonic organism, one would expect to find its skeletons distributed over different kinds of bottom and a very wide range of depths. However, its remains are found only on the small-particle bottoms to which it is confined in life by the special requirements of the larvae. Secondly, there is a direct relationship between the maximum depths at which *C. canariensis* has been observed in the various marine areas, and the temperature of the bottom water in those areas (see p. 189). Both these observations suggest that *C. canariensis* is a truly benthonic organism.

6. Minimum depth

Cupuladria canariensis occurs mainly on small-particle bottoms and is hence a full member of that rather select level-bottom community described by Petersen (cf. Thorson 1955). A type of small-particle bottom from which it is excluded, however, is one where the sand grains have a tendency to shift under the influence of water movements. The minimum depth at which the larvae of *C. canariensis* and other lunulitiform species, such as *Discoporella umbellata* (Defrance), can settle and develop into adult colonies therefore depends on the intensity of the water turbulence over the bottom, i.e. on the depth of the wave base and on the strength of the bottom currents. Since both these factors are determined by the degree of exposure of the shelf and by oceanographical factors, the minimum depth mentioned above varies from place to place (text-fig. 12).

Cupuladria colonies are therefore unlikely to be washed up on the shore, and there are no records that this has ever occurred, although 'one dead and worn' colony of *D. umbellata* has been found on the shore at Balboa, Panama Canal Zone (Hastings 1930, p. 718). As Stach (1936, p. 63) has put it, 'their free mode of life prohibits their existence in the littoral zone where wave action is strongly felt'. The lunulitiform Bryozoa thus seem to be confined to the *stable* small-particle bottoms below wave base. This conclusion is quite contrary to that of Darteville (1933, 1935), who inferred an agitated, current-infested biotope from the common occurrence of broken and regenerated lunulitiform colonies in the Eocene of Belgium. Yet there is no reason why fragmentation should be due solely to mechanical breakage in a highly turbulent environment; the destructive activity of other marine organisms in deeper, quieter water might just as easily be responsible (Ginsburg 1957, p. 83). It is known that holothurians (sea cucumbers) include the lunulitiform Bryozoa in their diet. Silén (1942, p. 13) records eight colonies of *C. canariensis* taken from the stomach of the sea-urchin *Meoma ventricosa*, and I have observed the occurrence of fragments and of several entire colonies of *C. canariensis* among the coarser debris in the stomach of a holothurian in the north-western Gulf of Mexico (Cavalier 1956 Station 227, at a depth of 37.5 fathoms). Darteville (1935) gives Recent examples of regenerated zoaria of *C. canariensis* (Pl. 25, fig. 5) taken from the Mediterranean locality Râs-el-Amouch at a depth of 45 fathoms, which is well below that at



TEXT-FIG 12. Minimum depths at which *Cupuladria canariensis* has been found in various areas. Notice shallowest occurrences in sheltered, deepest occurrences in exposed biotopes.

which sand transport could occur, let alone transport and breakage of far larger objects such as bryozoan colonies.

7. *Maximum depth (minimum temperature)*

The maximum depth of occurrence of *Cupuladria canariensis* is determined by the temperature of the bottom water. The maximum depths at which *C. canariensis* has been found in three marine provinces is as follows:

	Fathoms	
NW Gulf of Mexico	138	} Gulf of Mexico
NE Gulf of Mexico	117	
Straits of Florida	122	
Jamaica	150	} W and S confines of Sargasso Sea
E of Jacksonville, Florida	440	
N of St. Thomas, Virgin Islands	300-470	
Sénégal	118	} Equatorial West Africa
Nigeria	120	

Since the recent geographical distribution of *C. canariensis* is roughly limited both in the Atlantic and in the eastern Pacific by the 14° C. surface isocrymes (text-fig. 3) (and it must be remembered that the bottom water at shelf depths will be a few degrees colder) it may reasonably be assumed that this approaches the minimum temperature at which *C. canariensis* can survive. The maximum depths of occurrence and the corresponding bottom-water temperatures of approximately 12° C. observed in various marine areas seem to confirm this assumption (text-fig. 13).

The deep occurrences along the western and southern confines of the Sargasso Sea are of particular interest. In all three cases the data refer to living specimens. The hydrography of this region (text-fig. 14) is almost unique in featuring a lenticular body of water of uniform temperature (18° C.) and salinity (approx. 36.5‰) down to a depth of 300-400 metres (Worthington 1959). Below this depth a gradual decrease of temperature takes place down to the main thermocline. Clearly it is only the peculiar temperature conditions prevailing in this area that permit the occurrence of *C. canariensis* at such unusually great depths.

8. *Maximum temperature*

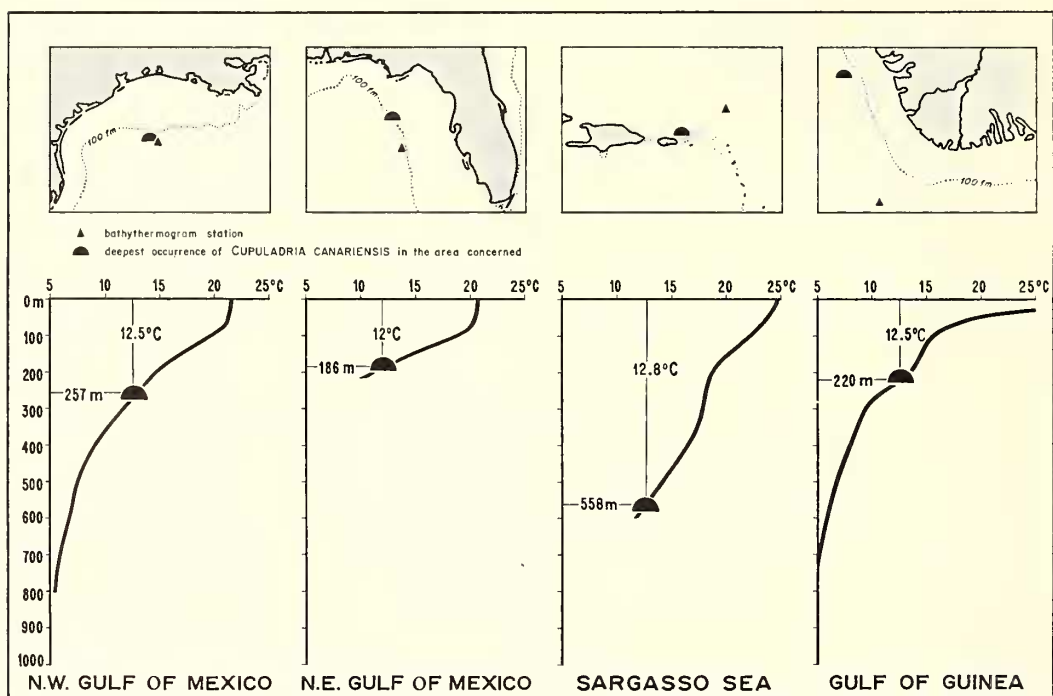
It is at the shallow end of its depth range that one has to seek the maximum temperature which the species will tolerate. This will be in shallow coastal waters, where the effects of atmospheric heat exchange are most strongly felt.

It will be readily understood, however, that the determination of this parameter will be far less precise than that of the minimum temperature, since the absolute maxima vary from year to year. Thus, *C. canariensis* may conceivably form part of the bottom fauna of a shallow bay during the normal summer of a particular year, but the following year an abnormally hot summer may bring its occupation of that bay to a sudden termination. The best approximation will therefore be found by taking the average maximum temperature in the warmest month, recorded over a number of years.

Areas where such shallow occurrences of *C. canariensis* coincide with the necessary amount of regularly recorded temperature data are Tampa Bay, Florida, and Breton

Sound, Louisiana, where *C. canariensis* occurs at minimum depths of 4 and 2 fathoms respectively (text-fig. 12).

According to the records published by the U.S. Coast and Geodetic Survey (1955), the average maximum temperature in the warmest month (July) for the years 1947–54 at St. Petersburg (Tampa Bay) was 31° C. Since this figure is based on surface measurements, the corresponding value for the shallow bottom water is bound to be somewhat less extreme.

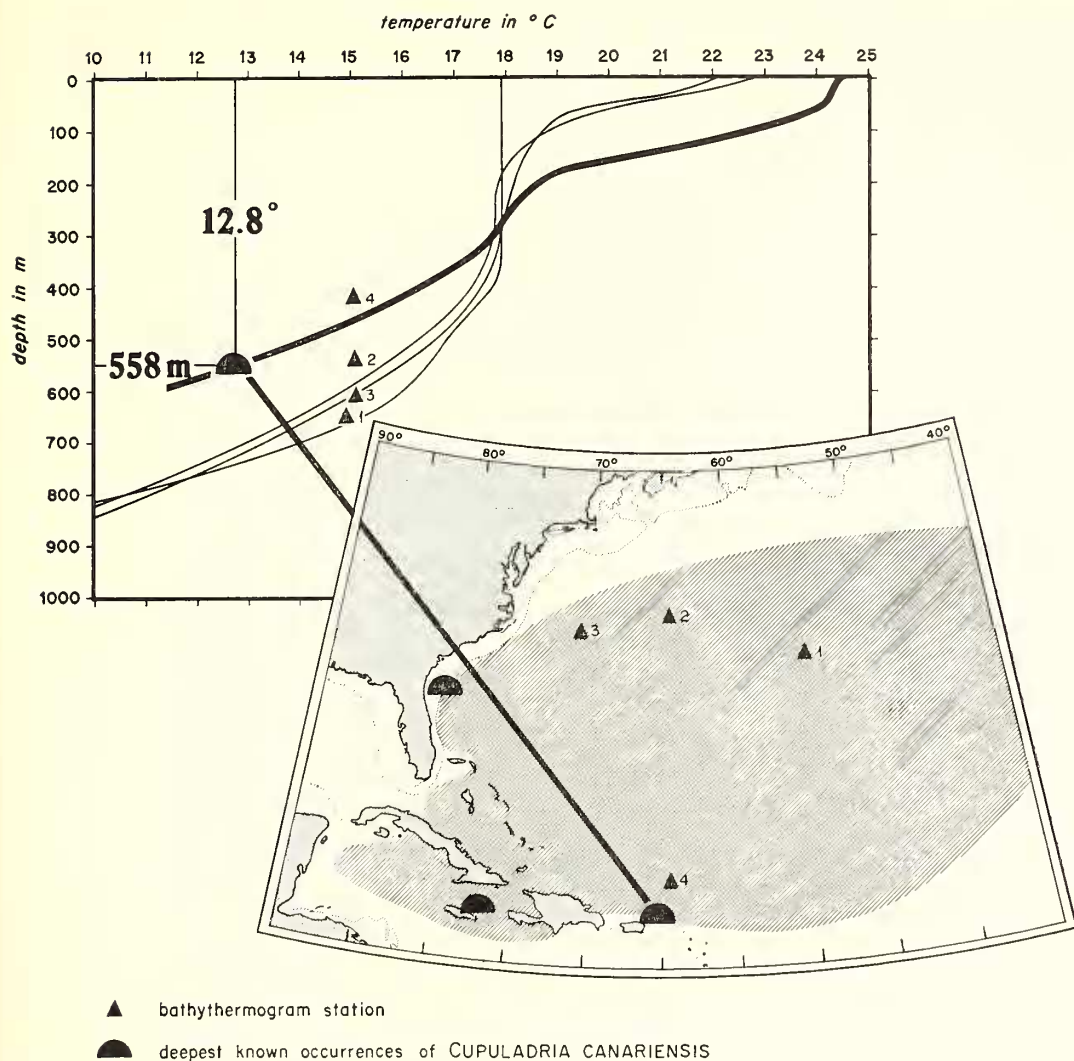


TEXT-FIG. 13. Relation between deepest occurrences of *Cupuladria canariensis* and bottom-water temperature.

In Breton Sound, where *C. canariensis* is known to occur in 2–3 fathoms depth in the lee of Breton Island (Parker 1956), surface-water temperatures during the summer reach an average absolute maximum of about 31–32° C. (Scruton 1956, p. 2937). According to Scruton (loc. cit.), ‘vertical stratification is stronger in the summer than at other times, so that bottom temperatures in Breton Sound proper probably seldom reach 32°.

9. Maximum salinity

The clue to the maximum salinity that *C. canariensis* will tolerate lies in the Mediterranean. From its occurrences elsewhere, on the Florida shelf and in the West Indies, one may infer that it still thrives in salinities of approximately 36.5‰. In the Mediterranean, on the other hand, salinities at the surface are everywhere higher than 37‰ (and increase with depth), except where the surface current carries water of Atlantic origin and an original salinity of about 36.25‰ through the Strait of Gibraltar along the



TEXT-FIG. 14. Deepest known occurrences of *Cupuladria canariensis* are found where deeply descending warm water mass of Sargasso Sea intersects with sea bottom. Shading in ocean area indicates the occurrence of water of 18° C. at 300 m. depth (map and graphs after Worthington 1959).

north coast of Africa as far east as Tunisia (Sverdrup, Johnson and Fleming 1960, pp. 643, 646).

The extent of this Atlantic water in the Mediterranean coincides exactly with the Recent Mediterranean distribution of *C. canariensis* (text-fig. 15d). The easternmost Mediterranean record of the species is from Cape Rosa, Algeria, 40 km. east of Bône. *C. canariensis*, like all other lunulitiform species, is conspicuously absent among the bryozoan fauna of the eastern Mediterranean, for example in Tunisia (Canu and Bassler 1930), Egypt (O'Donoghue and De Watteville 1939), and Syria (Gautier 1957). Since this entire area lies south of the 14° C. surface isocryme (text-fig. 15d) and since

bottom temperatures in the Mediterranean, even at great depths, nowhere drop below about 13° C. (Nielsen 1912; Furnestin 1960), it is clear that here the limiting factor is not the water temperature but the $>37\text{‰}$ salinity.

This conclusion has the interesting implication that the Miocene, Pliocene, and early Pleistocene Mediterranean (text-fig. 15a-c) was somewhat less saline than it is at present. The difference was most marked in the Sicilian, when *C. canariensis* (and by inference salinities $<37\text{‰}$) extended into the Levantine basin (Rhodes), where present-day salinities constantly remain about 39‰ (Wüst 1960, figs. 2, 5; pl. 7).

10. Minimum salinity

Data on the minimum salinity which *C. canariensis* will tolerate must be inferred from its occurrence in the shallow coastal waters, where precipitation and run-off are most effective in lowering the salinity.

Reduced salinities have been observed in the following shallow areas where *C. canariensis* is known to occur:

a. Breton Sound, leeward of Breton Island, Louisiana; depth 2-3 fathoms (Parker 1956); bottom salinity 28.5‰, measured in the autumn of 1951 during flood tide; the ebb tide produces still lower salinities (Scruton 1956, p. 2927).

b. South of Calcasieu Pass, Louisiana; depth 5.5 fathoms (text-fig. 12). Salinities measured at neighbouring stations (Bandy 1954, fig. 8, Sta. 106, Sta. 108) are of the order of 28-28.5‰. To all appearances these figures are based on surface measurements, but in this shallow turbulent part of the Gulf of Mexico vertical stratification is bound to be slight and the corresponding bottom salinities will therefore probably be not very different.

C. canariensis is absent in the Gulf of Mexico off Grand Isle, Louisiana, presumably because here salinities at 10 feet below the surface may drop periodically to as low as 21‰ in June and July, and 14‰ in February (Geyer 1950, p. 103). The lowest monthly average in this area is 22.6‰ (March 1949).

11. Recognition

Another, more subjective, factor which affects the boundaries of the known distribution of *C. canariensis* is the ease with which the species can be recognized. Large undamaged colonies may easily attain a diameter of 1.5 cm., and their aesthetically satisfying shape makes them conspicuous among the other members of the macro-fauna. Unfortunately, *C. canariensis* is rather fragile and during rough handling in nature or in

EXPLANATION OF PLATE 26

Fragments of fossil *Cupuladria canariensis* (Busk) from various localities.

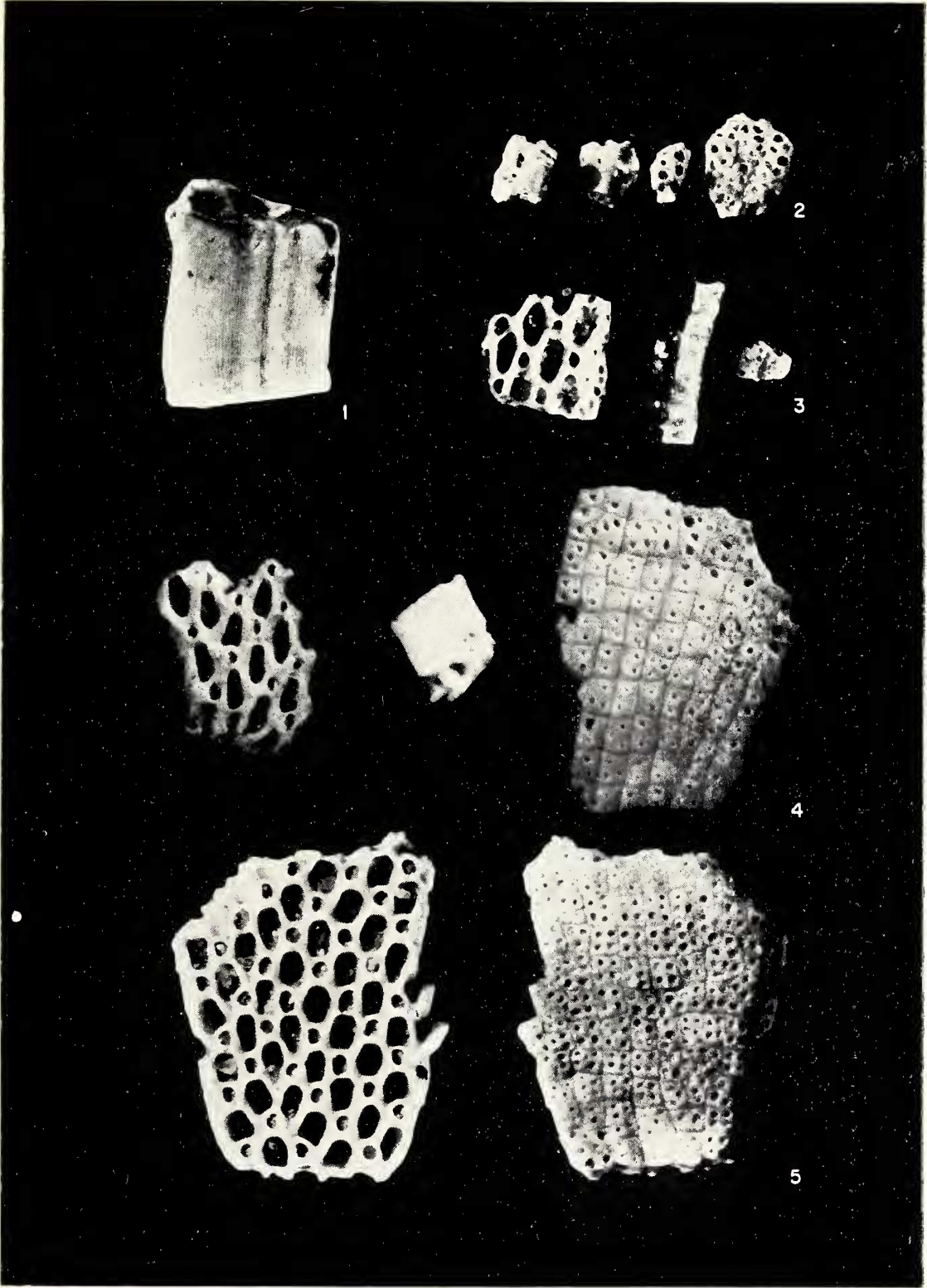
Fig. 1. Detail of the broken surface, showing the characteristic fine, parallel, vertical striation. Lower Miocene (Carapita formation) of Mene Grande Oil Company well SB-133, Estado Monagas, Venezuela, 3,825-3,840 ft. $\times 40$.

Fig. 2. Middle Miocene (Reinbek/Dingdener Stufe) of Twistringen, SSW of Bremen, Germany. $\times 20$.

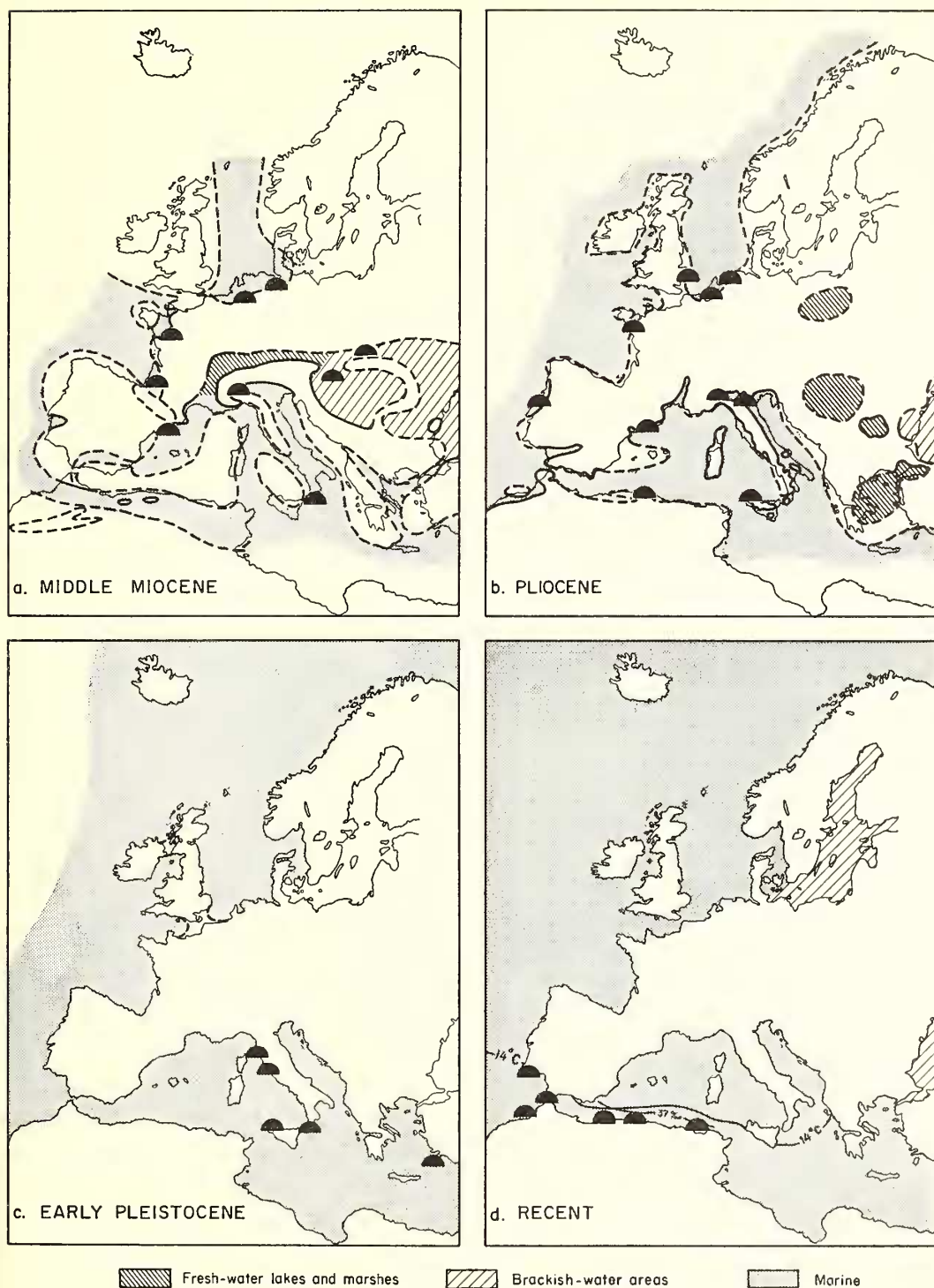
Fig. 3. Lower Miocene of Shell-BP Petroleum Development Company well Ituk-1, Nigeria, 3,320-3,780 ft. $\times 20$.

Fig. 4. Lower Miocene (Chickasawhay formation) of Limestone Creek, Wayne County, Mississippi, U.S.A. $\times 20$.

Fig. 5. Upper Miocene (Cubagua formation) of Socony Mobil Oil Company well Cubagua-1, Cubagua, Venezuela, 218 ft. $\times 20$.



LAGAATJ, *Cupuladria canariensis* (Busk)



TEXT-FIG. 15. Fossil and recent distribution of *Cupuladria canariensis* in Europe and North Africa (Middle Miocene and Pliocene base maps after Wills 1951).

the laboratory is apt to break, almost always along the radial lines on the concave surface. The smallest recognizable fragments take the form of tiny rectangular prisms (Pl. 26, fig. 1), whose dorsal ends correspond to the rectangular compartments visible on the concave surface (text-fig. 16). These compartments are perforated, and so, consequently, are the dorsal ends of the individual prisms. The vertical faces are flat and show fine, parallel, vertical striation (Pl. 26, fig. 1). Thus even very small fragments can be recognized (Pl. 26, figs. 2-5), and for this reason *C. canariensis* may be regarded as a component of both the macro- and the microfauna.

APPLICATIONS

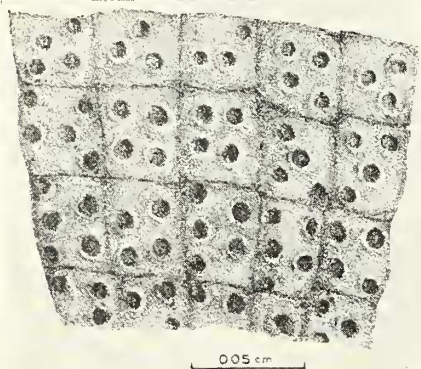
1. Shifts in sea-water temperature since the Miocene

Palaeobotany holds the key to the interpretation of Tertiary climates in north-west Europe. It is known that the north-west European climate gradually cooled from tropical (Eocene), through subtropical (Miocene and early Pliocene) to warm temperate (late Pliocene) conditions, after which even more marked and rapid cooling to subarctic conditions introduced the Pleistocene.

At present both summer and winter air temperatures in north-west Europe are strongly influenced by the temperature of the water in the eastern Atlantic and the North Sea. It is not unreasonable to assume, therefore, that the subtropical and oceanic climates prevailing in north-west Europe during the Miocene and Pliocene periods bore a direct relationship to considerably higher sea-water temperatures in these latitudes.

Such an hypothesis is strongly supported by a comparison of the present-day occurrences of *C. canariensis* with those during Miocene and Pliocene times (text-fig. 17). As has been already mentioned (p. 189), the northern boundary of its present area of distribution

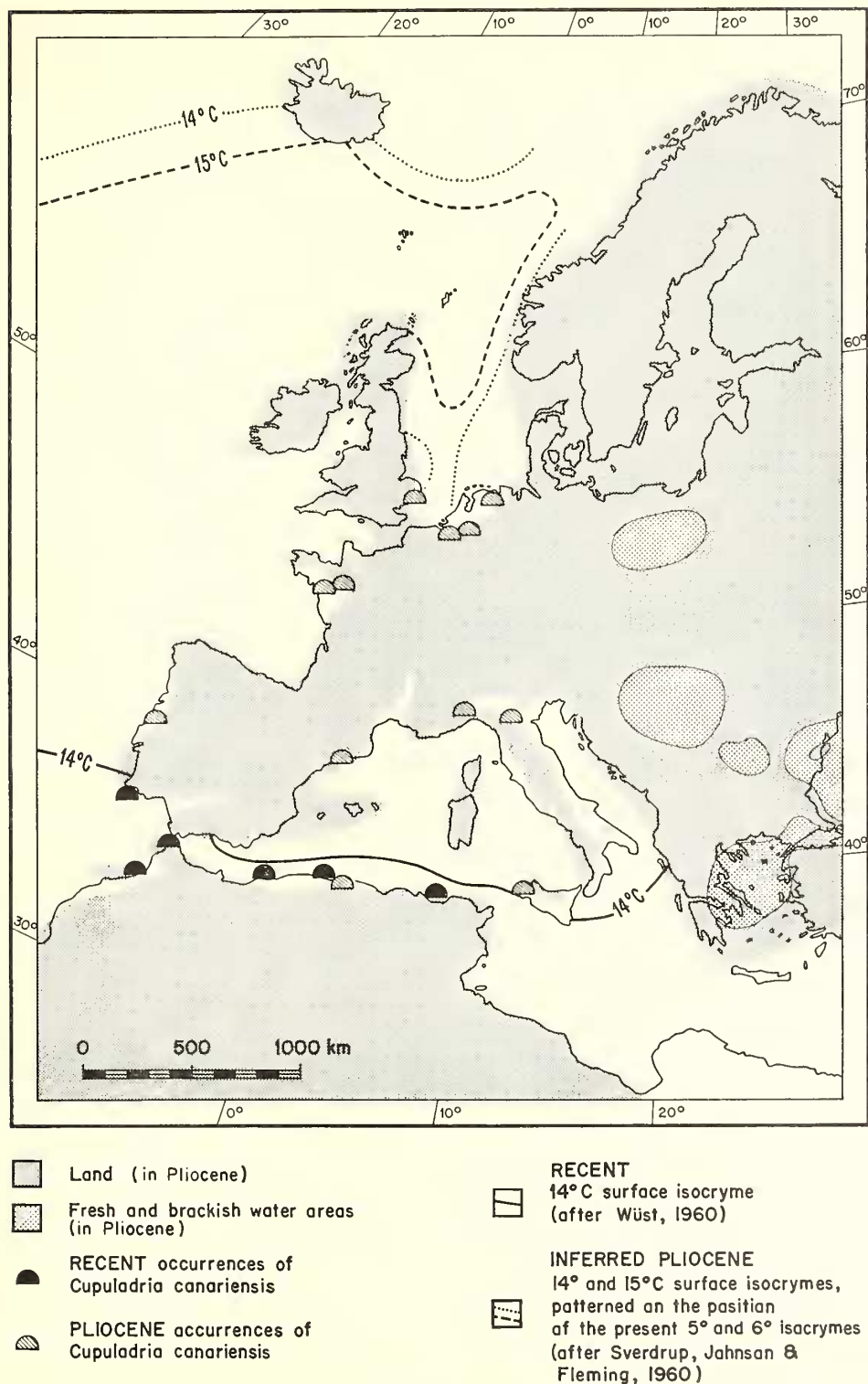
in the northern hemisphere coincides with the 14° C. surface isocryme (text-fig. 3). Consequently, Miocene and Pliocene winter surface-water temperatures in the North Sea basin must have been at least 14° C. February surface-water temperatures in this area now average between 5° and 6° C. (*vide* Sverdrup, Johnson, and Fleming 1960, chart II). In the Miocene and even in the Pliocene the water in the southern part of the North Sea must therefore have been at least 8° or 9° C. warmer than it is at present. This conclusion accords well with the figures derived by the Polish palaeobotanist Szafer for the amount by which Pliocene air temperatures in Europe north of the Alps exceeded those now prevailing:



TEXT-FIG. 16. *Cupuladria canariensis*. Detail of the concave surface (after Busk 1859a).

January +11°, July +9°, yearly average +9° C. (*vide* Godwin 1956, p. 296).

This conclusion is particularly interesting, however, because both in the Middle Miocene (text-fig. 15a) and in the Pliocene (text-fig. 15b) the land area at present occupied by the British Isles was connected to the continent of Europe. *C. canariensis* (and the entire warm-water fauna associated with it) must therefore have migrated to the North Sea area of those times by a path lying to the north of Scotland. In view of the present-



TEXT-FIG. 17. Shift of sea water temperatures in the Eastern Atlantic and Mediterranean since the Pliocene (Pliocene base map after Wills 1951).

day confinement of the species by the 14° C. surface isocryme, this isotherm must have lain to the north of Scotland in both the Miocene and Pliocene periods and probably resembled in shape the present-day 5° C. isocryme, which under the influence of the Gulf Stream curves around Scotland and penetrates into the North Sea (text-fig. 17). The stranding of a loggerhead turtle, *Caretta caretta* (Linn.), on the Norwegian coast in December 1951 (Willgoos 1953) and the capture of a flying fish, *Cypsilurus heterurus*, in Oslo Fiord in 1848 and in 1937 (Bruun 1938) are indications that even today the Gulf Stream occasionally carries tropical and subtropical marine organisms along this ancient migration route.

During the Pleistocene *C. canariensis* did not have a chance to migrate once more into the North Sea region (text-fig. 15c). This sea-water temperature did not rise sufficiently to allow this, even in the interglacial periods, when the climate was somewhat warmer than it is now. From the composition of the molluscan fauna of the Dutch Eemian (the last, late-Pleistocene, interglacial), van Straaten (1956, pp. 224, 225) concluded that the temperature of the sea-water at that time could only have been about 4° C. higher than that of the present North Sea, and might have been no more than 2° or 3° C. higher. It is interesting to note that Spaike (1958, p. 31) concluded that the southern element of this Eemian fauna must also have reached the Dutch coastal area by the route north of Scotland.

2. The Oligocene–Miocene boundary in the Gulf Coast and Caribbean areas

During the past decade, several attempts have been made to correlate the Tertiary formations on either side of the Atlantic. The problem of defining the Oligocene–Miocene boundary in the Caribbean area has been closely connected with these attempts and has still not definitely been solved.

A detailed discussion of this problem lies outside the scope of this paper. Those who are interested are referred to the paper by Eames (1953), through whose activity the problem became critical, to the ensuing discussion between Stainforth (1954) and Eames (1954), to the later restatement of the problem by Stainforth (1960a; 1960b, with extensive bibliography) and to the renewed discussion between Eames *et al.* (1960a; 1960b) and Stainforth (1960c). The arguments put forward by Eames *et al.* have now been stated in full detail in their book on Mid-Tertiary stratigraphical correlation (1962).

Briefly, the Oligocene–Miocene boundary in the Caribbean area has undergone a progressive lowering during the past decade. All concerned agree that this move was justified; there is no agreement, however, about the level in the Caribbean sequence of planktonic foraminiferal zones where this boundary should finally be drawn. Stainforth (1960b, p. 226) is undecided 'whether the whole *Globigerina ciperoensis* zone and part of the *Globigerina dissimilis* zone or only part of the *Globigerina ciperoensis* zone represents the whole Oligocene'. Eames (1955, p. 86), on the other hand, implied complete absence of marine Oligocene sediments in Trinidad by his statement that 'probably all the Cipero formation is of Lower Miocene age'. Eames *et al.* (1960a, 1960b, 1962) have since corroborated this view and have even extended it so that not only the Cipero but also the underlying San Fernando formation is included. If their opinion is correct, a major hiatus occurs in the Trinidad sequence between the Eocene (Navet and equivalents) and the Miocene (San Fernando, Cipero and equivalents) marine deposits.

It is important to discover whether, and to what extent, the lunulitiform Bryozoa, and in particular *Cupuladria canariensis*, throw light on the matter.

Lunulitiform Bryozoa, which range from the Upper Cretaceous to Recent, have long been of interest to palaeontologists. *Lunulites*, the eponymous genus, was introduced by Lamarck in 1816 and since then a considerable number of fossil species have been recorded from Tertiary and Quaternary strata both in Europe and in North America. The accompanying range charts (text-fig. 18) show the time-stratigraphic distribution of these species in the two hemispheres.

Comparison of these two charts reveals several interesting facts:

a. There are no Eocene and Oligocene species of *Lunulites* common to both hemispheres. It is possible that a thorough systematic revision of the group might alter this situation. But whether it would or not, it is significant that there is a similar lack of common species among the contemporaneous larger Foraminiferida of both hemispheres.

b. The disappearance of the genus *Lunulites* clearly did not take place contemporaneously in both hemispheres. In North America it probably no longer occurs *in situ* in the post-Vicksburg formations, whereas in Europe it persists into the Pliocene. It should be borne in mind, however, that several living species of *Lunulites* have been recorded from Australian seas.

c. Several names common to both charts, of which one is *C. canariensis*, first appear in the Miocene of Europe and in the post-Vicksburg formations of the southern U.S.A. This new appearance of modern lunulitiform genera and species, which, as has been seen in the case of *C. canariensis*, possess exceptional environmental tolerance leading to wide and rapid dispersal, may well serve as a criterion for establishing the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic.

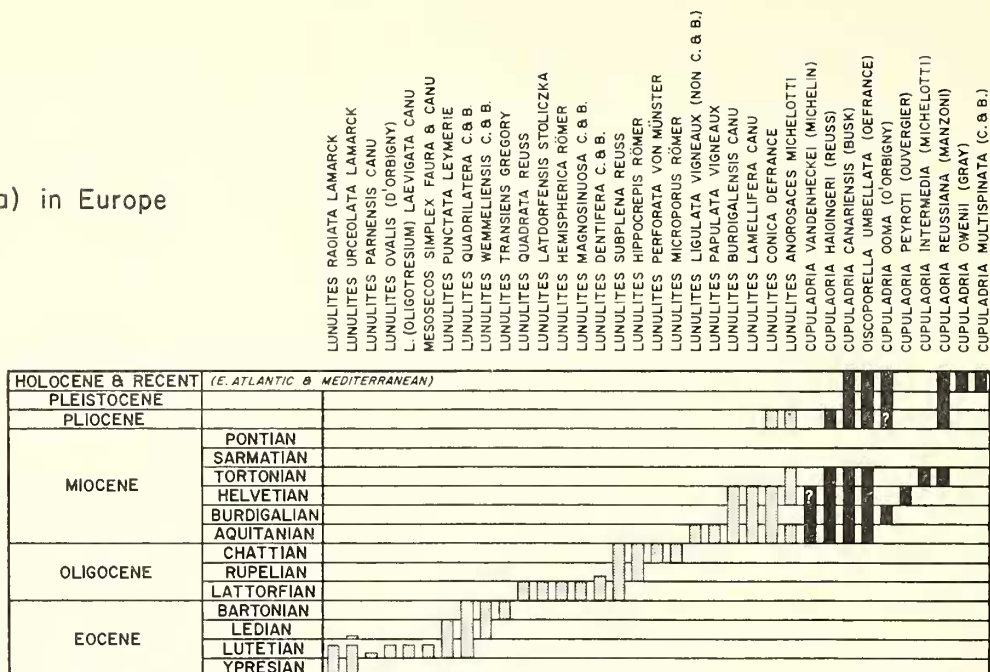
By this criterion the Vicksburg group correlates with some part of the European Oligocene (absolute hegemony of *Lunulites*), whereas such post-Vicksburg formations as the Chickasawhay of Mississippi and Alabama and the subsurface Upper Frio of Texas cannot be considered older than Aquitanian (since both contain *C. canariensis*). Although most North American stratigraphers, e.g. Cooke *et al.* (1943), MacNeil (1944), and oil companies do not share this view, it is clear that it was held as long ago as 1934 by others, such as Howe (1934) and McGuirt (1941).

Some of the evidence underlying text-fig. 18b is brought out in greater detail on the correlation chart of the Gulf Coast Oligocene and Miocene formations (text-fig. 19), which shows the known occurrences of the genus *Lunulites* and *C. canariensis* according to the published records and my own observations. Conspicuous on this chart is the wide distribution of these lunulitiform Bryozoa throughout the marine Tertiary sediments, even though information on several southern states is still incomplete.

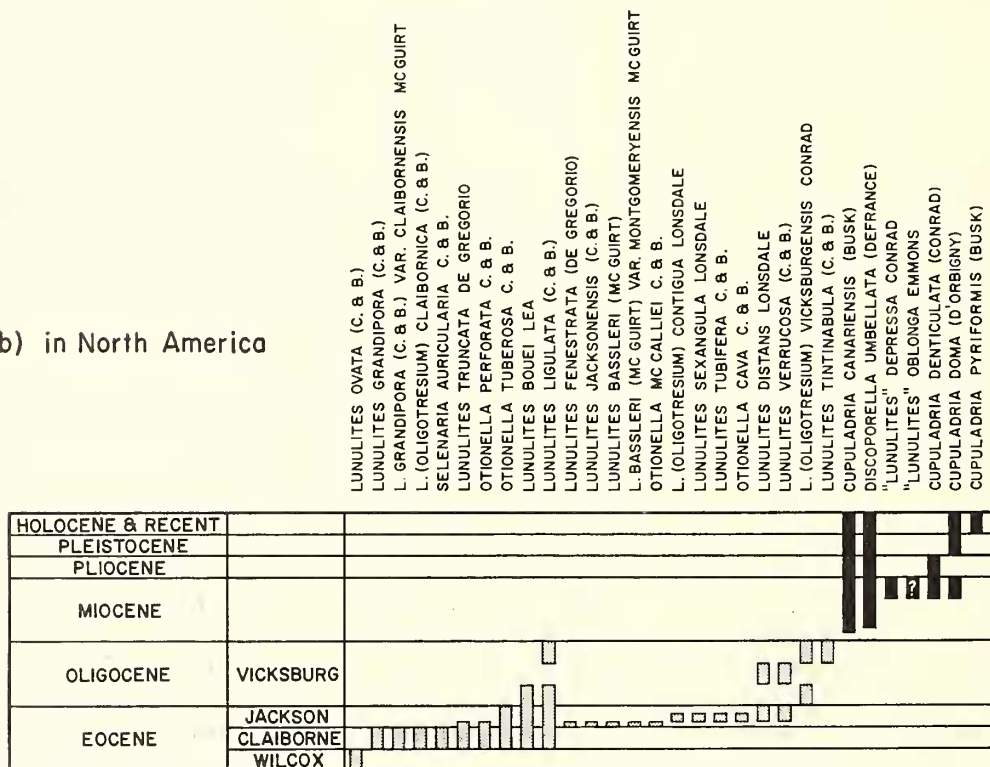
It is interesting to study the Caribbean area in the light of what is known about Europe and the Gulf Coast, where modern lunulitiform species and genera first appear in the Aquitanian and post-Vicksburg formations respectively.

It has already been shown (text-fig. 9) that lunulitiform Bryozoa, in this case *C. canariensis*, are widely distributed throughout the 'Oligocene–Miocene' basin of eastern Venezuela. The vertical distribution of *C. canariensis* in various parts of the basin is

a) in Europe



b) in North America



TEXT-FIG. 18. Time-stratigraphic distribution of Tertiary and Quaternary lunulitiform species.

shown in text-fig. 20. As far as the problem of the Oligocene–Miocene boundary is concerned, the oldest occurrences are the most relevant.

In northern Guarico the earliest occurrence is to be found in the upper part of the ‘Oligocene’ Roblecito formation of well GXB-5. In the Rio Areo of northern Monagas *C. canariensis* occurs at the base of the Areo Shale, directly above its contact with the Los Jabillos formation (text-fig. 21). The Areo Shale is generally considered to be the lateral equivalent of the lower part of the Naricual formation of the Barcelona area,

		S. TEXAS	LOUISIANA	W. MISSISSIPPI	E. MISSISSIPPI	SW. ALABAMA	NW. FLORIDA	
PLIO-CENE?		GOLIAO	"CITRONELLE FM."	"CITRONELLE FM."	"CITRONELLE FM."	CITRONELLE FM. (Type)	"CITRONELLE FM."	
MIOCENE		LAGARTO		PASCAGOULA CLAY	PASCAGOULA CLAY	PASCAGOULA CLAY	CHOCOTAW STAGE ALUM BLUFF STAGE ARCA YOLDIA SHOAL RIVER OAK GROVES CANCELLARIA FACIES ECOPORA CHIPOLA HATHORN	
		OAKVILLE	FLEMING CLAY	HATTIESBURG CLAY	HATTIESBURG CLAY	HATTIESBURG CLAY		
		CATAHOULA FM.			CATAHOULA FM.	PAYNES HAMMOCK FM.		TAMPA LIMESTONE
		ANAHUAC UPPER FRIO LOWER FRIO	CATAHOULA FM.	CATAHOULA FM.	CHICKASAWHAY FM.	CHICKASAWHAY FM.		
OLIGOCENE VICKSBURG GROUP					BUCATUNNA CLAY	BUCATUNNA CLAY	SUWANNEE LIMESTONE	
		VICKSBURG	VICKSBURG GROUP	MARIANNA EQUIVALENT	MARIANNA LST.	MARIANNA LST.	MARIANNA LST.	
			MINT SPRING MARL LENTIL	MINT SPRING MEMBER OF MARIANNA	MINT SPRING MEMBER OF MARIANNA			
				FOREST HILL SAND	FOREST HILL	RED BLUFF CLAY	RED BLUFF CLAY EQUIVALENT	
		LUNULITES SPP.				CUPULORIA CANARIENSIS		

LUNULITES SPP.

CUPULADRIA CANARIENSIS

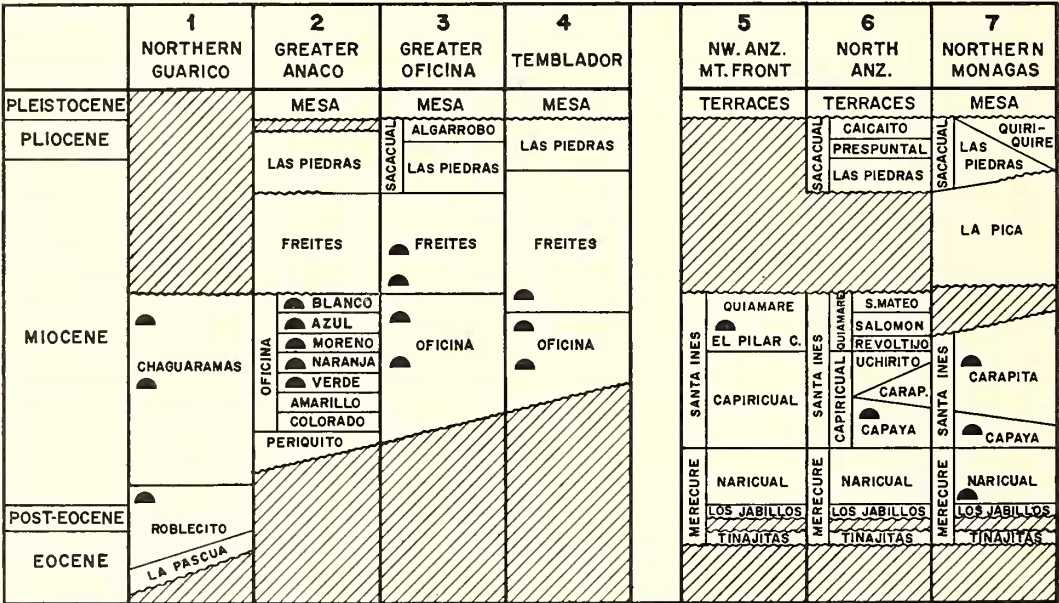
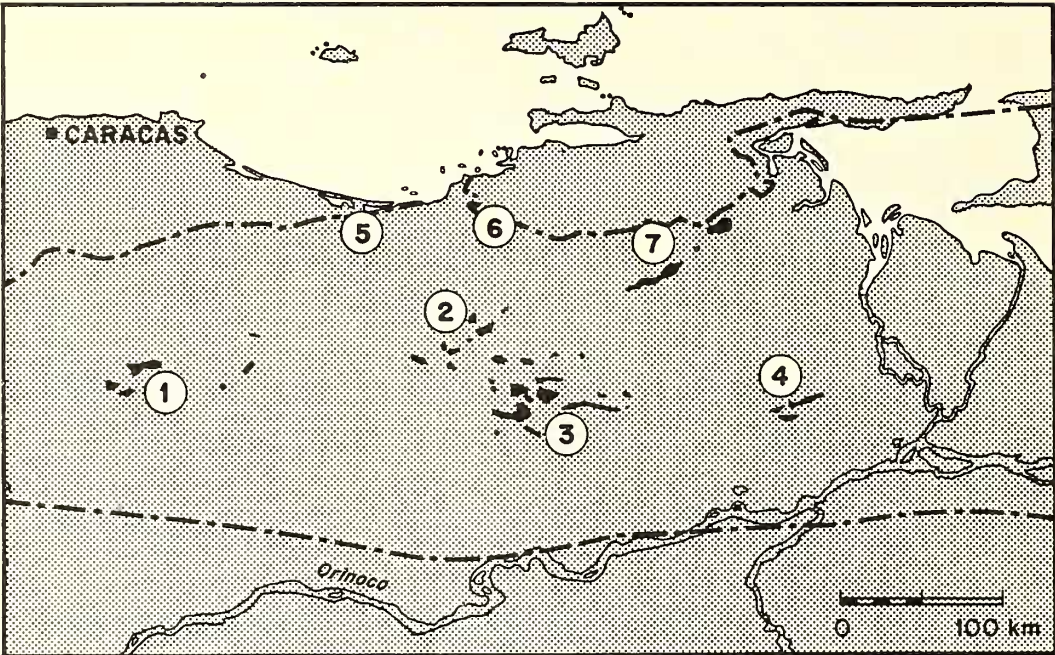
TEXT-FIG. 19. Occurrences of *Lunulites* spp. and of *Cupuladria canariensis* throughout the Oligocene and Miocene formations of the Gulf Coast.

which itself was considered to be of Lower Oligocene, and possibly even Upper Eocene, age (Renz *et al.* 1958, p. 576). This age assessment can no longer be maintained. Since they contain *C. canariensis*, both the upper part of the Roblecito and the Areo Shale (and for that matter the Naricual) cannot be of more than Aquitanian (or post-Vicksburg) age. The correctness of this interpretation is reinforced by the fact that *C. canariensis* is accompanied in both cases by *Discoporella umbellata*, another ‘modern’ lunulitiform species.

It is interesting to compare these occurrences with the Caribbean planktonic foraminiferal zonation locally established by the Creole Petroleum Corporation.

According to Creole, the Areo Shale represents the upper two-thirds of the *Globorotalia opima opima* zone and the whole of the *Globigerina ciperoensis ciperoensis* zone. The oldest known occurrences of *C. canariensis* at the base of the Areo Shale thus fall in the lower half of the *G. opima opima* zone.

The underlying Los Jabillos formation has hitherto generally been considered as Upper Eocene (*vide* Feo-Codecido 1956, p. 331; Renz *et al.* 1958, p. 576). This age assessment, too, needs revision in the light of newly acquired evidence. According to Creole, the Los Jabillos formation must be post-Eocene, since its stratigraphical position falls slightly above the base of the *G. opima opima* zone.



▲ CUPULADRIA CANARIENSIS

TEXT-FIG. 20. Occurrences of *Cupuladria canariensis* throughout the Tertiary formations in the eastern Venezuela basin (map and correlation chart after Renz *et al.* 1958, modified).

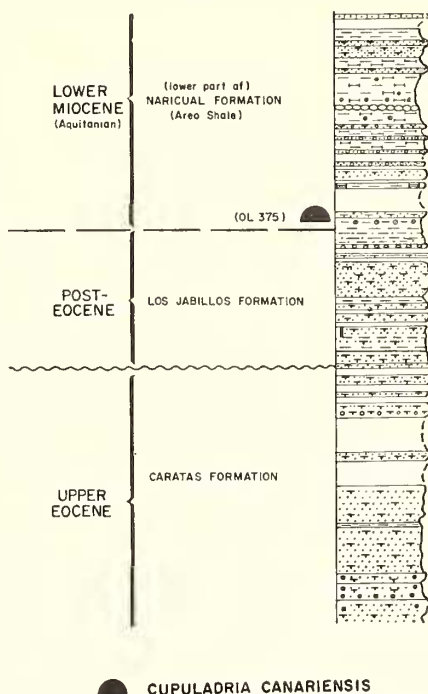
Again according to Creole, the Los Jabillos formation is in turn underlain by shales with *Globigerina ampliapertura* (not present in the Rio Areo outcrop section shown in text-fig. 21). It is this *G. ampliapertura* zone that on planktonic foraminiferal evidence correlates with the Vicksburg (Bolli 1957, p. 107). Thus one might expect to find a different suite of lunulitiform Bryozoa at this level. Unfortunately, there are no earlier records of this group of Bryozoa from Eastern Venezuela than those mentioned above. All one can say is that the Vicksburg, as it is defined in the southern U.S.A., is characterized, from the point of view of the lunulitiform bryozoan sequences, by the absolute hegemony of the genus *Lunulites* (text-fig. 18b) and therefore correlates with some part of the European Oligocene (text-fig. 18a). This would imply that the *G. ampliapertura* zone is also Oligocene.

In summary it appears that Eames *et al.* were substantially correct in lowering the Oligocene-Miocene boundary in the Caribbean area farther than any of their critics were prepared to go. From the presence of modern lunulitiform Bryozoa it must be concluded that at least the upper two-thirds of the *Globorotalia opima opima* zone is Miocene (Aquitanian or younger). On the other hand, Eames *et al.* (1960a, p. 448; 1962, pp. 48, 49, fig. 5) would definitely seem to be going too far in wishing to submit the Vicksburg to the same rejuvenation course. The Vicksburg lunulitiform bryozoan assemblages have a distinct Oligocene character, and if the planktonic foraminiferal correlation is correct, this would imply that the *Globigerina ampliapertura* zone of the Caribbean sequence of planktonic foraminiferal zones is also Oligocene. The Oligocene-Miocene boundary in the Caribbean, subject of so much discussion in the past decade, would thus be pinpointed in eastern Venezuela somewhere between the top of the *Globigerina ampliapertura* zone and the top of the lower one-third of the *Globorotalia opima opima* zone.

The earliest occurrences of *C. canariensis* in Nigeria of which I am aware have so far been found in the wells Ituk-1 (range 3,320–3,780 feet) (Pl. 26, fig. 3) and Ituk-2 (range 2,770–2,950 feet) in the Calabar flank area, and in Ihuo-1 (range 2,062–2,085 feet).

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TEXT-FIG. 21. Earliest occurrence of *Cupuladria canariensis* in the Rio Areo outcrop section, northern Monagas, eastern Venezuela (from unpublished Company reports); 1:5,000.

The Dutch manuscript was translated by Mr. R. W. Burke; Mr. W. B. Mulder executed the text figures with great care; Messrs. J. Fournier and J. H. H. van Gigch took some of the photographs.

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APPENDIX

1. *Synonymy*

- 1959a *Cupularia canariensis* BUSK, G. On some Madeiran Polyzoa. Collected by J. Yates Johnston, Esq. Zoophytology. *Quart. J. micr. Sci.* **7**, 66, pl. 23, figs. 6–9.
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- 1868 *Cupularia canariensis* Busk: MANZONI, A. *Saggio di Conchiologia foss. Subappennina*, p. 71.
- 1869 *Cupularia canariensis* Busk: MANZONI, A. Bryozoi Pliocenici Italiani. *S.B. Akad. Wiss. Wien*, **59**, p. 26, pl. 2, fig. 17.
- 1873 *Membranipora canariensis* (Busk): SMITT, F. A. Floridan Bryozoa collected by Count L. F. De Pourtales. II. *Kungl. Svenska Vetensk.-Akad. Handl.* **11**, p. 10, pl. 2, figs. 69–71.
- 1877a *Cupularia canariensis* Busk: MANZONI, A. I bryozoi fossili del Miocene d'Austria ed Ungheria. II. *Denkschr. Akad. Wiss. Wien*, **37**, p. 72, pl. 17, fig. 56.
- 1877b *Cupularia canariensis* Busk: MANZONI, A. Bryozoaires du Pliocène supérieur de l'île de Rhodes. *Mém. Soc. géol. Fr. (3)*, **1**, p. 67.
- 1878 *Cupularia canariensis* Busk: BROECK, E. VAN DEN. Esquisse géologique & paléontologique des dépôts pliocènes des environs d'Anvers. *Ann. Soc. Malac. Belg.* **9** (1874), p. 274.
- 1879 *Cupularia canariensis* Busk: SEGUENZA, G. Le formazioni terziarie nella provincia di Reggio (Calabria). *Mem. Accad. Lincei (3)*, **6**, pp. 131, 371.
- 1881 *Cupularia canariensis* Busk: COPPI, F. *Paleontologia modenese o guida al paleontologo*. Modena, p. 123.

- 1885 *Lunulites conica* DeFrance var. *depressa*: LORIÉ, J. Contributions à la géologie des Pays-Bas. Résultats géologiques et paléontologiques des forages de puits à Utrecht, Goes et Gorkum. *Arch. Mus. Teyler* (2), **2**, p. 133, pl. 3, figs. 15a, b.
- 1887 *Cupularia canariensis* Busk: PERGENS, E. Pliocène Bryozoën von Rhodos. *Ann. naturh. (Mus.) Hofmus.* **2**, p. 31.
- 1889 *Cupularia canariensis* Busk: WATERS, A. W. Supplementary Report on the Polyzoa collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. Sci. Res. Voy. Challenger, Zoology*, **31**, pt. 79, p. 36.
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- 1891 *Cupularia canariensis* Busk: NEVIANI, A. Contribuzione alla conoscenza dei briozoi fossili italiani. Briozoi postpliocenici del sottosuolo di Livorno. *Ibid.* **10**, p. 130.
- 1894 *Cupularia canariensis* Busk: BROECK, E. VAN DEN. Matériaux pour la connaissance des dépôts pliocènes supérieurs rencontrés dans les derniers travaux de creusement des Bassins Maritimes d'Anvers, Bassin Africa (ou Lefebvre) et Bassin America. *Bull. Soc. belge Géol.* **6** (1892), p. 139.
- 1895a *Cupularia canariensis* Busk: NEVIANI, A. Briozoi fossili della Farnesina e Monte Mario presso Roma. *Palaeontogr. ital.* **1**, p. 101.
- 1895b *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, I. *Boll. Soc. Romana Studi Zool.* **4**, pp. 238, 243.
- 1895 *Cupularia canariensis* Busk: DE ANGELIS, J. Descripción de los Briozoos fósiles pliocénicos de Cataluña. Barcelona, p. 9, pl. B, figs. 6–9.
- 1896 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, III. *Boll. Soc. Romana Studi Zool.* **5**, p. 121.
- 1898 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, V. *Ibid.* p. 38.
- 1900 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi terziari e posterziari della Toscana. *Boll. Soc. geol. ital.* **19**, p. 362.
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- 1907 *Cupularia canariensis* Busk: CALVET, L. Bryozoaires. *Expéd. sci. 'Travailleur' et 'Talisman' 1880–1883*, **8**, p. 393.
- 1908 *Cupularia canariensis* Busk: CANU, F. Iconographie des Bryozoaires fossiles de l'Argentine. *An. Mus. nac. B. Aires*, **17**, p. 275, pl. 5, figs. 8–10.
- non 1908 *Cupularia canariensis* Busk: ROBERTSON, A. The incrusting chilostomatous Bryozoa of the west coast of North America. *Univ. Calif. Publ. Zool.* **4**, p. 314, pl. 24, figs. 90, 91 = *Discoporella umbellata* (DeFrance).
- 1909 *Cupularia guineensis* Busk: NORMAN, A. M. The Polyzoa of Madeira and neighbouring islands. *J. Linn. Soc. (Zool.)*, **30**, p. 289, pl. 37, figs. 2–6 (non *Cupularia guineensis*: Busk, G. Catalogue of Marine Polyzoa in the Collection of the British Museum, **2** (1854), p. 98, pl. 114, figs. 1–5).
- 1913a *Cupularia canariensis* Busk: CANU, F. Contributions à l'étude des Bryozoaires fossiles. IV. Pliocène d'Alger. *Bull. Soc. géol. Fr.* (4), **13**, p. 124.
- 1913b *Cupularia canariensis* Busk: CANU, F. Contributions à l'étude des Bryozoaires fossiles. X. Astien de Valle Andona. *Ibid.*, p. 128.
- 1914 *Cupularia guineensis* Busk: OSBURN, R. C. The Bryozoa of the Tortugas Islands, Florida. *Publ. Carnegie Instn.* **182**, p. 194 (non *Cupularia guineensis*: Busk, G. Catalogue of Marine Polyzoa in the Collection of the British Museum, **2** (1854), p. 98, pl. 114, figs. 1–5).
- 1914 *Cupularia canariensis* Busk: FAURA, M. Sobre la presencia de un briozoo vivente, la *Cupularia canariensis* descubierto en los terrenos miocénicos de Cataluña. *Bol. Soc. esp. Hist. nat.* **14**, p. 397.
- 1916 *Cupularia canariensis* Busk: FAURA, M. and CANU, F. Sur les Bryozoaires des terrains tertiaires de la Catalogne. *Treb. Inst. catal. Hist. nat.* p. 77, text-figs. 4a, b, pl. 3, figs. 7, 8.
- 1917 *Cupularia canariensis* Busk: CANU, F. Les Bryozoaires fossiles des Terrains du Sud-Ouest de la France. X. Burdigalien. *Bull. Soc. géol. Fr.* (4), **16** (1916), p. 137, pl. 3, figs. 4–6.

- 1919a *Cupularia canariensis* Busk: CANU, F. and BASSLER, R. S. Bryozoa of the Canal Zone and related areas. *Bull. U.S. nat. Mus.* **103** (1918), p. 119, pl. 53, figs. 5-7.
- 1919b *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Fossil Bryozoa from the West Indies. *Publ. Carnegie Instn.* **291**, p. 78, pl. 1, figs. 8-10.
- 1920a *Cupuladria canariensis* (Busk): CANU, F. Contributions à l'étude des Bryozoaires fossiles. XV. Redonnien du Pigeon-Blanc (Loire-Inférieure). *Bull. Soc. géol. Fr.* (4), **19** (1919), p. 213.
- 1920b *Cupuladria canariensis* (Busk): CANU, F. Contributions à l'étude des Bryozoaires fossiles. XVI. Scaldisien d'Anvers. *Ibid.*, p. 213.
- 1920 *Cupuladria canariensis* (Busk): DUVERGIER, J. Note sur les Bryozoaires du Néogène de l'Aquitaine. *Act. Soc. linn. Bordeaux*, **72**, p. 149.
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- 1921 *Cupularia canariensis* Busk: WATERS, A. W. Observations upon the relationships of the (Bryozoa) Selenariadae, Conescharellinidae, &c., fossil and Recent. *J. Linn. Soc. (Zool.)*, **34**, p. 410 (partim), pl. 29, figs. 1-5; pl. 30, figs. 11, 12, 21, 22, 25.
- 1923 *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. North American Later Tertiary and Quaternary Bryozoa. *Bull. U.S. nat. Mus.* **125**, p. 28, pl. 1, figs. 7-9.
- 1923 *Cupuladria biporosa* CANU, F. and BASSLER, R. S. North American Later Tertiary and Quaternary Bryozoa. *Ibid.*, p. 29, pl. 47, figs. 1, 2.
- 1924 *Cupuladria canariensis* (Busk): CIPOLLA, F. I briozoi del Quaternario inferiore dei dintorni di Palermo. Nota preliminare. *Boll. Soc. Sci. nat. econ. Palermo*, **6**, p. 7.
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2. Documentation of maps and figures

All cited papers are listed in either the References or the Synonymy.

BMNH: British Museum (Natural History).

USNM: United States National Museum.

KSEPL: Koninklijke/Shell Exploratie en Produktie Laboratorium, Volmerlaan 6, Rijswijk Z.H., Netherlands.

TEXT-FIG. 3. The selected localities shown are:

	Reference or repository		Reference or repository
1. Cape Rosa, Algeria	BMNH	3. Oran, Algeria	Waters 1921
2. Râs-el-Amouch, Algeria	Dartevelle 1935	4. Tangier Bay	BMNH

	<i>Reference or repository</i>		<i>Reference or repository</i>
5. Vanneau Sta. XXIX, Morocco	Canu and Bassler 1925b	28. Lat. 28° 4' N, long. 93° 44' W, 40 fms.	KSEPL
6. Cape Sagres, Portugal	BMNH	29. Lat. 25° 47' N, long. 96° 27' W, 50 fms.	KSEPL (ex Mr. R. W. Barker)
7. Off Punta Delgada, Azores	Silén 1942	30. Albatross Sta. 2361, NE of Cabo Catoche	USNM
8. Madeira	Busk 1859a; Norman 1909; Silén 1942	31. Port Antonio, Jamaica	USNM
9. 'entrée de la Bocayna', Canary Islands	Calvet 1907	32. Caroline Sta. 55, Samaná Bay, Santo Domingo	USNM
10. Gran Canaria, Canary Islands	Silén 1942	33. Off Guanica Harbor, Puerto Rico	Osburn 1940
11. Lat. 27° 16' N, long. 23° 21' W	Silén 1942	34. St. Thomas, West Indies	Silén 1942
12. Cap Blanc, Mauritania	Calvet 1907	35. St. Martin, West Indies	Silén 1942
13. Cape Verde, Sénégal	BMNH	36. Albatross Sta. 2145, NNW of Aspinwall	Silén 1942
14. Conakry, Guinée	BMNH	37. Cape la Vela, Colombia	Osburn 1947
15. Petit Tahou, Liberia	Waters 1889, 1921	38. Aruba, Netherlands Antilles	Osburn 1947
16. Accra, Ghana	BMNH	39. Tortuga Island, Venezuela	Osburn 1947
17. SE of Lagos, Nigeria, 13 fms.	KSEPL	40. Margarita Island, Venezuela	Osburn 1947
18. Off Fishtown River, Nigeria, 14 fms.	KSEPL	41. Barbados, West Indies	BMNH
19. N of Fernando Poo, 42 fms.	KSEPL	42. Lat. 9° 28' N, long. 60° 8' W, 39 fms.	KSEPL (ex Dr. D. J. Nota)
20. Calypso Sta. 45, W of Libreville, Gabon	BMNH	43. Berbice, British Guiana	BMNH
21. Albatross Sta. 2597, off Cape Hatteras	USNM	44. Off Bahía, Brazil	Waters 1889
22. Albatross Sta. 2415, E of Jacksonville, Fla.	USNM	45. Cedros Island, Lower California	Osburn 1950
23. Albatross Sta. 2639, Straits of Florida	Canu and Bassler 1928a	46. Albatross Sta. 3012, Gulf of California	USNM
24. Tortugas, Florida	Smitt 1873; Osburn 1914; Silén 1942	47. Albatross Sta. 2826, Gulf of California	Canu and Bassler, 1929
25. Albatross Sta. 2405, off Cedar Keys, Fla.	Canu and Bassler 1928a	48. Clarion Island, Mexico	Osburn 1950
26. S of Mobile, Alabama	Parker 1956	49. Socorro Island, Mexico	Osburn 1950
27. Lat. 28° 40' N, long. 90° 14' W, 19 fms.	KSEPL	50. West coast of Mexico	Osburn 1950
		51. West coast of Costa Rica	Osburn 1950
		52. West coast of Panama	Osburn 1950
		53. Gorgona, Colombia	Hastings 1930
		54. Galapagos Islands	Osburn 1950
		55. Ecuador	Osburn 1950

TEXT-FIG. 4. The selected localities shown are:

Miocene

1. Twistringcn, SSW of Bremen, Germany	Reinbek/Dingdener Stufe, Middle Miocene (Pl. 26, fig. 2)	ex Dr. C. W. Drooger
2. Beeringen, Netherlands	Diepboring 15, 154-159 m., Middle Miocene	Lagaaij 1953
3. Wyneghem, near Antwerp, Belgium	Lower Diestian (Deurnian), Upper Miocene	Lagaaij 1952
4. Vienna Basin, Austria	Tortonian, Middle Miocene	Manzoni 1877a; Canu and Bassler 1925a
4a. Benczyn, near Wadowice, Poland	Tortonian, Middle Miocene	Malecki 1951
5. Turin, Italy	Miocene	Scotti 1936
6. Reggio, Calabria, Italy	Tortonian, Middle Miocene	Seguenza 1879
7. Ferrière l'Arçon, Indre-et-Loire, France	Pontilevian, Middle Miocene	Canu and Lécointre 1925; Buge 1957
8. Dept. Gironde, France	Aquitanian and Burdigalian, Lower Miocene	Canu 1917; Duvergier 1920; Vig-neaux 1949
9. Barcelona province, Spain	Helvetian, Middle Miocene	Faura 1914; Faura and Canu 1916

10. Niger Delta, Nigeria	Exploration well Oloibiri-1, 9,560-9,570', Miocene	KSEPL
11. Calabar area, Nigeria	Exploration well Ituk-1, 3,320-3,780', Miocene (Pl. 26, fig. 3)	KSEPL
12. Misselle River, 10 km. N of Tiko, E of Mount Cameroon, Nigeria	Lower Miocene	KSEPL
13. French Cameroons	Middle Miocene	KSEPL
14. Monroe County, Florida	Caloosahatchee formation, Miocene	Canu and Bassler 1919 <i>b</i> ; 1923
15. Jackson's Bluff, Ochlockonee River, Leon County, Florida	Choctawhatchee, Miocene	Canu and Bassler 1919 <i>b</i> ; 1923
16. Shell Bluff, Shoal River, N of Mossyhead, Walton County, Fla.	Shoal River (type locality), Miocene	KSEPL
17. Limestone Creek, Wayne County, Mississippi	Chickasawhay, Miocene (Pl. 26, fig. 4)	KSEPL (ex Mr. R. W. Barker)
18. East Baton Rouge Parish, Louisiana	Superior Oil Prod. Company's Duplantier Community No. 1 well, 7,671-7,687', <i>Heterostegina</i> zone; 8,091-8,101', <i>Marginulina</i> zone, Catahoula formation, Miocene	McGuirt 1941
19. Laguna Atorcosa, Cameron County, Texas	Shell-Continental Fee $\# 1$, 11,810-11,850', <i>Marginulina</i> zone, Miocene	KSEPL (ex Dr. D. D. Bannink)
20. Goliad County, Texas	Housh, Thompson & Crown Central C. G. Wood $\# 1$, 3,163-3,193', updip limit of Anahuac shale wedge, Miocene	Shell Oil Company, Corpus Christi Division
21. Gulf of Mexico, off Nueces County, Texas	Gulf Oil Corp. and others, Block 889, 3-A, 10,300', Upper Frio, Miocene	KSEPL (ex Mr. E. M. Wilkins)
22. Bowden, Jamaica	Bowden Beds, upper Middle Miocene	Canu and Bassler 1919 <i>a</i> ; 1919 <i>b</i> ; 1923
23. Cercado de Mao, Santo Domingo	Middle Miocene	Canu and Bassler 1919 <i>b</i> ; 1923
24. Port Limón, Costa Rica	Middle Miocene	Canu and Bassler 1923
25. Rio Coro, at Caujarao, Distr. Miranda, Estado Falcon, Venezuela	Caujarao formation, upper Middle Miocene	KSEPL
26. Cabo Blanco, near Maiquetía Airport, Distr. Federal, Venezuela	Playa Grande formation, Upper Miocene	KSEPL
27. Estado Guarico, Venezuela	Creole Petroleum Corp., GXB-5, Roblecito formation, Miocene	Compañía Shell de Venezuela, Caracas
28. Estado Anzoategui, Venezuela	Mene Grande Oil Company, OG-1, 2,125'; 3,250', Freites formation; 3,750-4,625', Oficina formation, Miocene	Compañía Shell de Venezuela, Caracas
29. Estado Monagas, Venezuela	Creole Petroleum Corp., ORC-2, 3,900-4,200', Carapita formation, Miocene	Compañía Shell de Venezuela, Caracas
30. Estado Monagas, Venezuela	Compañía Shell de Venezuela, Cerro Negro-3, Freites formation; Oficina formation, Miocene	Compañía Shell de Venezuela, Caracas
31. Cubagua Island, Venezuela	Socony Mobil Oil Company, Cubagua-1, 218', Cubagua formation, Upper Miocene (Pl. 26, fig. 5)	KSEPL
32. Concord quarry, Point à la Pierre, Trinidad	Concord marl, Miocene	KSEPL (ex Dr. E. Th. N. Spiker)

Pliocene

I. Sutton, Suffolk, England	Gedgravian, Pliocene	Busk 1859 <i>b</i>
II. Antwerp, Belgium	Scaldisian (prob. Luchtbal horizon), Pliocene	Canu 1920 <i>b</i>
III. Heumensoord, Netherlands	Boring 1928, 102·40–109·00 m., 'Scaldisian', Pliocene	Lagaaij 1952
IV. Roden, Netherlands	Boring 114/23, 184·50–215·00 m., Pliocene	KSEPL (ex Dr. J. H. van Voort-huysen)
V. Contigné, Maine-et-Loire, France	Redonian, Pliocene	Roger and Buge 1946; Buge 1957
VI. Pigeon-Blanc (Landreau), near Nantes, France	Redonian, Pliocene	Canu 1920 <i>a</i> ; Roger and Buge 1946; Buge 1957
VIIa. Pombal, Portugal	Pliocene	Galopim de Carvalho 1961
VII. El Ampurdan, near Barcelona, Spain	Pliocene	De Angelis 1895
VIII. Valle Andona, Asti, Piedmont, Italy	Astian, Pliocene	Manzoni 1869; Canu 1913 <i>b</i>
IX. Province of Modena, Italy	Plaisancian, Pliocene	Namias 1890
X. Altavilla, near Palermo, Sicily, Italy	Pliocene	Cipolla 1921
XI. Nador, near Algiers, Algeria	Plaisancian, Pliocene	Canu 1913 <i>a</i>
XII. Terrebonne Parish, Louisiana	Terrebonne Gas Company Fee #1, 2,300', Pliocene	McGuirt 1941
XIII. Minnitimmi Creek, Bocas Island, Almirante Bay, Panama	Pliocene	Canu and Bassler 1928 <i>a</i>
XIV. Camarones, 10 km. E of Esmaralda, Ecuador	Pliocene	KSEPL (ex Mr. J. Brouwer)

Pleistocene

A. Livorno, Italy	Sicilian, Pleistocene	Neviani 1891
B. Monte Mario and Farnesina, near Rome, Italy	Calabrian	Manzoni 1869; Neviani 1895
C. Carrubare, Calabria, Italy	Sicilian?	Neviani 1905
D. Palermo, Sicily, Italy	Sicilian?	Cipolla 1924
E. Rhodes	Sicilian	Manzoni 1877 <i>b</i> ; Pergens 1887; Silén 1942
F. Gulf of Mexico, Mississippi River Delta area, Louisiana	South Pass, Block 6 Area, State Lease 2590 1, 500–1,100', 'Upper Marine', Pleistocene	KSEPL (ex Mr. J. J. Gouty)
G. Gulf of Mexico, High Island area	Federal Block A–104, Shell-Continental 'Neptune–1', 775–790'; 835–1,000', Pleistocene	KSEPL
H. Gulf of Mexico, off Matagorda County, Texas	Ohio Oil Company, State of Texas 403 #1, 537–599'; 662–754'; 1,935–1,997', Pleistocene	KSEPL
J. Cabo Blanco, near Maiquetía Airport, Distr. Federal, Venezuela	Mare formation, Pleistocene?	KSEPL
K. Estado Monagas, Venezuela	Compañía Shell de Venezuela, Guanipa–1, 640–670', Paria formation, Pleistocene	Compañía Shell de Venezuela, Caracas
L. Puerto Militar, Bahía Blanca, Argentine	Pampéan, Pleistocene	Canu 1908

TEXT-FIG. 5. Sources: (a) Collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk, Netherlands; (b) Parker 1956; and (c) various other sources (see list):

	Lat. N	Long. W	Depth in fms.		Lat. N	Long. W	Depth in fms.
1. Cavalier 1956 Sta. 128	29°02'54"	89°28'26"	5-5	47. Atlantis 1951 Sta. 168	28°51'30"	83°39'30"	12
2. Parker 1956 Sta. 410	29°27'	89°15'	2	48. 169	28°54'	83°34'30"	11-5
3. 321	29°30'30"	89°15'	2	49. 170	28°55'	83°28'30"	11
4. 322	29°30'30"	89°10'	2	50. 171	28°56'30"	83°22'	8
5. G. 2074	29°30'	88°52'	7-5	51. 172	28°58'	83°16'30"	7?6?
6. Parker 1956 Sta. 346	29°24'	88°54'	10	52. 173	28°59'	83°12'30"	5
7. 349	29°22'	88°51'	15	53. Off Egmont Key, Florida	27°36'27"	83°08'57"	11-5
8. 316	29°12'	88°43'	39	54.	27°36'27"	83°04'48"	10-5
9. G. 2021	29°09'	88°43'	43	55.	27°36'27"	83°02'42"	8-5
10. G. 2028, Sandpile Bank	20°04'40"	88°43'	49	56.	27°36'27"	83°00'30"	8-5
11. Parker 1956 Sta. 311	29°22'	88°32'	32	57.	27°36'27"	82°53'48"	7
12. 309	29°23'	88°22'	30	58.	27°36'27"	82°51'42"	5-5
13. 308	29°26'	88°20'	30	59. Tampa Bay, Florida	27°38'09"	82°37'27"	4-5
14. 244	29°26'	88°08'	29	60.	27°39'54"	82°36'06"	5-5
15. U.S.S. Hydrographer 1941/2, Sta. 50	29°46'05"	86°58'	103-8	61.	27°41'14"	82°34'43"	4-5
16. U.S.S. Hydrographer 1941/2, Sta. 23	29°31'	86°26'	77	62.	27°46'	82°31'36"	4
17. U.S.S. Hydrographer 1941/2, Sta. 45	29°33'	86°08'	21	63. Vema-3 1954 BT # 18	27°08'	83°30'	23
18. U.S.S. Hydrographer 1941/2, Sta. 40	30°15'	86°11'	15	64. Albatross 1885 Sta. 2409 (Silén 1942)	27°04'	83°21'15"	26
19. U.S.S. Hydrographer 1941/2, Sta. 39	30°13'	86°08'	12-5	65. Vema-3 1954 Dredge # 2	26°50'	83°40'	29
20. Off Panama City, Florida	30°05'58"	85°45'39"	10	66. SSW of John's Pass, Florida	26°25'	83°32'	34
21.	30°01'24"	85°51'54"	14-5	67. Vema-3 1954 BT # 2	26°10'	84°20'	96
22.	30°00'45"	85°52'45"	15	68. Vema-3 1954 Dredge # 1	25°50'	84°30'	117
23. Albatross 1885 Sta. 2405 (Canu and Bassler 1928a)	28°45'	85°02'	30	69. Tortugas, Florida (Os- burn 1914)			10
24. Fish Hawk Sta. 7157 (USNM)	29°23'	83°41'45"	9	70. SW of Tortugas, Florida (Silén 1942)			40 m.
25. Off Cedar Keys, Florida	28°58'48"	83°16'42"	5-5	71. Rebecca Shoal, Florida (Silén 1942)			15 m.
26.	29°00'06"	83°15'	5	72. Albatross 1885 Sta. 2315 (Silén 1942)	24°26'	81°48'15"	37
27.	29°01'24"	83°13'20"	4-5	73. NW of Sombbrero Key, Florida	24°39'36"	81°04'12"	6-5
28.	29°02'36"	83°11'38"	4	74. S of Sombbrero Key, Flo- rida	24°35'30"	81°06'55"	25
29.	29°03'55"	83°09'50"	3-5	75. SE of Molasses Reef Light, Fla.	24°54'	80°15'30"	122
30.	29°05'16"	83°08'	3-5	76. Albatross 1886 Sta. 2639 (Canu and Bassler 1928a)	25°04'50"	80°15'10"	56
31. Atlantis 1951 Sta. 152	28°09'	85°07'	100	77. Due E of Carysfort Light, Fla.	25°13'15"	80°07'	78
32. 153	28°11'30"	85°02'	80	78. Off Turtle Harbor, Flo- rida (USNM)			20
33. 154	28°14'	84°57'	64	79. Due E of Triumph Reef, Fla.	25°28'30"	80°05'45"	45
34. 155	28°16'30"	84°52'	43	80. Due E of Triumph Reef, Fla.	25°28'30"	80°05'	58
35. 156	28°19'	84°46'30"	32	81. Off Fowey Light, Florida	25°30'48"	80°03'36"	80
36. 157	28°22'	84°14'	34	82. Fowey Light, Florida (Canu and Bassler 1928a)			40
37. 158	28°24'30"	84°36'	33				
38. 159	28°27'	84°31'	28				
39. 160	28°30'	84°25'30"	25				
40. 161	28°32'	84°20'	22				
41. 162	28°35'	84°14'	20				
42. 163	28°38'	84°08'	20				
43. 164	28°41'	84°02'	17				
44. 165	28°43'30"	83°56'	17				
45. 166	28°46'	83°50'	16				
46. 167	28°49'	83°44'	14				

TEXT-FIG. 6. Sources: (a) Collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk, Netherlands; (b) Parker 1956:

				Depth in fms.					Depth in fms.
		Lat. N	Long. W				Lat. N	Long. W	
1.	Cavalier 1956 Sta. 12	28°43'18"	95°19'09"	9	35.	Cavalier 1956 Sta. 307	28°09'30"	93°43'15"	35.5
2.	 20	28°47'30"	95°15'24"	10	36.	 306	28°16'15"	93°42'15"	35
3.	 21	28°45'16"	95°15'24"	10.5	37.	 305	28°22'12"	93°40'30"	30
4.	 23	28°42'47"	95°14'30"	12	38.	 304	28°29'06"	93°38'30"	24
5.	 28	28°37'03"	95°09'54"	15	39.	 303	28°37'24"	93°36'24"	18.5
6.	 30	28°34'50"	95°08'05"	16	40.	 302	28°43'	93°34'45"	15
7.	 35	28°44'48"	95°08'05"	11.5	41.	 301	28°49'	93°33'15"	12.5
8.	Univ. of Houston, Nos. 1-4	28°40'	94°33'	15	42.	 300	28°52'30"	93°32'	11
9.	Vema-3 1954 Core # 65 (Top 12")	28°10'48"	94°15'	30	43.	 299	28°59'15"	93°30'15"	11
10.	Heald Bank, N of Heald Bank Light			8.5	44.	 298	29°06'	93°28'12"	11
11.	Heald Bank	29°04'	94°14'	10.5	45.	 297	29°11'30"	93°26"	9
12.	Cavalier 1956 Sta. 331	29°03'15"	94°18'45"	6.5	46.	 296	29°15'09"	93°24'08"	8.5
13.	 330	29°01'06"	94°18'45"	8	47.	Sabine Bank area, Sta. 2	29°19'20"	93°36'30"	7
14.	 329	28°58'45"	94°18'45"	6	48.	Cavalier 1956 Sta. 294	29°21'04"	93°21'18"	8.5
15.	 328	28°55'42"	94°18'06"	11.5	49.	 293	29°23'48"	93°20'04"	6.5
16.	 327	28°49'36"	94°16'42"	13.5	50.	 292	29°24'42"	93°20'	7
17.	 326	28°43'44"	94°14'54"	15	51.	 291	29°26'24"	93°19'55"	4
18.	High Island area, Block A-104	28°42'12"	94°01'36"	15.5	52.	 290	29°27'28"	93°19'50"	6.5
19.	Cavalier 1956 Sta. 325	28°37'06"	94°13'14"	18	53.	 289	29°30'21"	93°19'38"	6.5
20.	 324	28°33'	94°12'15"	20	54.	 288	29°33'30"	93°19'26"	6.5
21.	 323	28°26'06"	94°10'30"	23	55.	 286	29°40'35"	93°19'40"	5.5
22.	 321	28°17'30"	94°08'30"	27.5	56.	 273	28°31'30"	91°49'15"	24
23.	 320	28°15'24"	94°03'54"	31.5	57.	 278	28°05'15"	91°58'	38
24.	 319	28°09'06"	94°00'00"	38	58.	 236	28°42'24"	90°59'38"	7
25.	 318	28°02'54"	93°51'30"	40	59.	 235	28°39'50"	90°59'38"	8.5
26.	 317	27°58'45"	93°49'45"	50	60.	 217	28°33'12"	90°59'50"	14
27.	 316	27°54'15"	93°47'45"	50	61.	 226	28°08'30"	91°01'	56
28.	 315	27°48'45"	93°45'30"	92	62.	 227	28°06'30"	91°01'	37.5
29.	 314	27°44'12"	93°43'48"	138	63.	 229	28°04'	91°01'	57
30.	 312	27°48'	93°47'36"	102	64.	 166	28°37'	90°16'12"	21.5
31.	 311	27°51'30"	93°47'	70	65.	 175	28°10'	90°13'30"	66
32.	 310	27°53'45"	93°46'30"	60	66.	 180	28°39'55"	90°13'45"	19
33.	 309	27°56'15"	93°46'	57	67.	 128	29°02'54"	89°28'26"	5.5
34.	 308	28°04'	93°44'20"	40	68.	Parker 1956, Sta. 410	29°27'	89°15'	2
					69.	 321	29°30'30"	89°15'	2
					70.	 322	29°30'30"	89°10'	2
					71.	 346	29°24'	88°54'	10

TEXT-FIG. 7. Source: samples kept at KSEPL, Rijswijk, Netherlands; the co-ordinates and depths are listed below:

				Depth in fms.					Depth in fms.
Mees Cremer 1959 Stations		Lat. N	Long. E		Mess Cremer 1959 Stations		Lat. N	Long. E	
1	158	6°11'20"	3°21'26"	44	16	206	5°24'01"	4°39'51"	120
2	320	6°20'04"	3°29'14"	13	17	133	5°19'58"	5°01'29"	16
3	169	6°18'24"	3°34'22"	19	18	137	5°12'46"	4°46'59"	109
4	168	6°20'31"	3°46'15"	14	19	310	4°54'09"	5°08'26"	25
5	170	6°11'50"	3°32'04"	42	20	311	4°48'55"	5°02'55"	45
6	162	6°07'25"	3°30'01"	63	21	312	4°47'34"	5°01'38"	55
7	163	6°08'45"	3°33'22"	52	22	107	4°37'17"	5°24'22"	12
8	164	6°10'24"	3°37'26"	44	23	108	4°34'47"	5°21'18"	18
9	171	6°11'25"	3°37'12"	43	24	109	4°32'19"	5°18'04"	29
10	165	6°12'00"	3°42'32"	41	25	377	4°24'10"	5°35'49"	10
11	318	6°11'01"	3°46'21"	47	26	376	4°23'33"	5°33'53"	11
12	215	6°13'59"	4°11'38"	12	27	375	4°23'01"	5°32'04"	13
13	147	6°05'40"	4°25'41"	21	28	374	4°22'34"	5°29'53"	14
14	212	5°42'43"	4°40'30"	37	29	373	4°22'07"	5°27'58"	17
15	203	5°32'00"	4°49'38"	27	30	372	4°21'41"	5°25'58"	21

<i>Mees Cremer</i>				<i>Depth</i>	<i>Mess Cremer</i>				<i>Depth</i>
<i>1959 Stations</i>		<i>Lat. N</i>	<i>Long. E</i>	<i>in fms.</i>	<i>1959 Stations</i>		<i>Lat. N.</i>	<i>Long. E</i>	<i>in fms.</i>
31	371	4°21'14"	5°23'58"	27	76	291	3°50'04"	6°43'19"	67
32	299	4°25'07"	5°34'55"	9	77	77	4°13'41"	6°47'27"	9
33	300	4°21'56"	5°31'46"	13	78	78	4°14'05"	6°51'59"	9
34	301	4°18'26"	5°27'29"	21	79	79	4°14'41"	6°56'58"	8
35	96	4°15'39"	5°42'55"	9	80	11	4°08'46"	7°01'31"	16
36	97	4°12'28"	5°40'38"	12	81	6	4°06'46"	7°00'54"	20
37	98	4°09'20"	5°38'25"	14	82	10	4°02'31"	7°02'05"	29
38	99	4°05'44"	5°35'37"	17	83	7	4°00'31"	7°01'12"	36
39	100	4°02'10"	5°33'06"	26	84	404	3°56'30"	6°58'42"	48
40	101	3°59'55"	5°31'23"	34	85	334	4°11'18"	7°18'47"	15
41	220	4°06'56"	5°37'31"	16	86	335	4°05'35"	7°18'12"	22
42	221	4°04'50"	5°40'50"	17	87	338	3°46'57"	7°18'17"	91
43	222	4°00'55"	5°43'11"	18	88	243	4°14'41"	7°35'01"	10
44	223	3°57'06"	5°45'07"	23	89	244	4°10'18"	7°34'56"	17
45	224	3°52'51"	5°47'47"	31	90	245	4°05'55"	7°34'59"	25
46	395	4°04'34"	5°50'10"	14	91	246	4°01'37"	7°34'54"	32
47	396	4°04'09"	5°52'23"	14	92	247	3°57'16"	7°34'56"	42
48	397	4°02'47"	5°54'24"	14	93	260	3°50'30"	7°30'10"	76
49	398	4°01'25"	5°56'21"	15	94	248	3°51'58"	7°35'00"	71
50	399	4°00'37"	5°58'38"	15	95	259	3°48'34"	7°39'49"	93
51	400	3°59'54"	6°00'59"	16	96	274	4°16'25"	7°42'38"	9
52	401	3°58'57"	6°03'18"	18	97	23	4°15'58"	8°01'50"	12
53	402	3°58'17"	6°05'42"	21	98	24	4°11'50"	8°02'33"	14
54	403	3°57'27"	6°07'50"	23	99	31	3°57'38"	8°04'39"	36
55	388	4°06'28"	6°02'25"	10	100	28	3°55'27"	8°05'30"	42
56	389	4°04'40"	6°01'34"	12	101	29	3°51'43"	8°05'49"	68
57	390	4°02'41"	6°00'52"	13	102	32	3°56'07"	8°08'35"	40
58	391	4°00'49"	6°00'08"	14	103	34	3°52'40"	8°18'02"	49
59	392	3°59'01"	5°59'32"	16	104	36	3°49'19"	8°17'22"	100
60	393	3°57'10"	5°58'58"	22	105	255	3°47'59"	8°20'19"	62
61	394	3°55'37"	5°58'24"	24	106	37	3°47'02"	8°20'17"	91
62	83	4°10'39"	6°10'25"	7	107	73	4°05'38"	8°26'10"	22
63	387	4°08'44"	6°06'38"	8	108	72	4°05'21"	8°30'16"	26
64	84	4°05'41"	6°07'53"	11	109	254	3°52'38"	8°28'02"	40
65	85	4°02'49"	6°07'04"	14	110	38	3°44'50"	8°23'50"	75
66	86	4°00'14"	6°06'26"	17	111	39	3°43'08"	8°27'22"	56
67	87	3°56'42"	6°05'02"	23	112	46	4°06'34"	8°34'35"	34
68	81	4°09'13"	6°18'27"	9	113	45	4°03'36"	8°36'10"	31
69	344	4°11'11"	6°26'59"	8	114	44	3°58'36"	8°35'43"	36
70	345	4°04'33"	6°26'11"	15	115	43	3°54'05"	8°35'01"	41
71	346	3°57'37"	6°24'40"	31	116	42	3°48'53"	8°33'59"	44
72	74	4°12'31"	6°31'22"	8	117	41	3°44'39"	8°33'01"	44
73	287	4°10'19"	6°43'14"	11	118	40	3°40'36"	8°32'11"	44
74	288	4°06'16"	6°43'20"	18	119	70	3°48'10"	8°43'41"	42
75	289	4°00'11"	6°43'24"	32					

TEXT-FIG. 8. Distribution of Pliocene marine facies after van Voorthuysen 1956, fig. 26. Eighteen borings and outcrop localities listed in Lagaij 1952, p. 33, are shown, to which the following occurrences north of the Rhine have here been added:

Wanneperveen-2	Kernboring NAM	171-50-224-50 m.
Oud-Appelscha		187-25-201-00 m.
Roden	114/23	191-50-213-00 m.